ALLEE EFFECTS, HOST TREE DENSITY AND THE ESTABLISHMENT OF INVASIVE BARK BEETLES

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“The design of a book is the pattern of a reality controlled and shaped by the mind of the writer. This is completely understood about poetry or fiction, but it is too seldom realized about books of fact. And yet the impulse which drives a man to poetry will send another man in to the tide pools and force him to try to report what he finds there. Why is an expedition to Tibet undertaken, or a sea bottom dredged? Why do men, sitting at a microscope, examine the calcareous plates of sea-cucumber, and, finding a new arrangement and number, feel an exaltation and give the new species a name, and write about it possessively.”

-John Steinbeck, 1951, The Log From the Sea of Cortez

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Abstract

The aim of this thesis was to understand the role of Allee effects and dispersal during the establishment and spread phases of bark beetle invasion events, a topic currently central to invasion ecology. Allee effects are defined as a positive relationship between population size and fitness. It has long been proposed that establishment probability and spread potential is dependent on propagule pressure, but few empirical studies have directly tested this hypothesis. I investigated the establishment potential and dispersal capabilities of bark beetles across large geographical scales in New Zealand and the United States of America. My overarching hypothesis was that bark beetle species in two different feeding guilds (saprophytic and secondary) would have different Allee thresholds, affecting their establishment and spread success.

In New Zealand, I found that two saprophytic bark beetles (*Hylurgus ligniperda and Hylastes ater*) were capable of dispersing at least 25 km from the nearest host Pinus patch through a fragmented and geographically complex landscape. The observations help to explain the widespread distribution of these insects throughout both the North and South Islands. Point introduction experiments of *H. ligniperda* in open (field) and closed (tent) environments revealed component Allee effects during both the colonization and larval development stages, leading to a demographic Allee effect. However, even the smallest releases (N = 10 *H. ligniperda*) sometimes resulted in colonization, indicating the high invasion potential of this insect species.

In the USA, both regional host density and an estimated Allee threshold helped explain the spatial distribution of a secondary bark beetle, *Ips pini*, through a heavily fragmented agricultural landscape. A large emergence pulse of I. pini in spring lifted disjunct populations over the estimated Allee threshold, apparently allowing the beetle to persist in the landscape at intermediate host densities. The colonization probability of I. pini was also positively related to the number of beetles released (a component Allee effect), but a strong negative density-dependent interaction during larval development offset this so there was no demographic Allee effect.

This work provides baseline data for theoretical ecologists modelling Allee effects, conservation ecologists conducting re-introductions, invasion ecologists concerned with future introductions of non-native species and policy makers targeting higher risk bark beetle species.

Chapter 1 - General Introduction

Allee effects

Some species of animals have to intraspecifically cooperate in order to survive (Courchamp et al. 1999). Animals huddle together in winter to keep warm and stay protected from predators (e.g. caribou and bobwhite quails) (Allee et al. 1949). Predatory pack animals (e.g. African wild dogs, hyenas and lions) collaborate as a pack to hunt, protect young and defend territory from other packs (Courchamp et al. 2000). Stable colonies of ants are maintained by the cooperation of a caste system involving workers and queens (Luque et al. 2013).

When population growth becomes negative below a threshold in which the cooperative benefits of a social structure becomes unviable, that population is likely to go extinct. This result is known as the Allee effect (Allee 1931; Allee 1938; Allee 1948; Odum 1953) and is technically defined as "a positive relationship between any component of individual fitness and either numbers or density of conspecifics" (Stephens et al. 1999). Factors potentially leading to an Allee effect when populations are small include heavier predation, not being able to find a mate, lack of pollination, sperm limitation, foraging inefficiency, loss of environmental conditioning, inbreeding and higher levels of genetic drift (Dennis 1989; Fowler and Baker 1991; Courchamp et al. 2008; Kanarek and Webb 2010).

Allee effects are divided into two categories: component and demographic Allee effects. Component Allee effects are relegated as the positive relationship between population density and a single component of individual fitness (e.g. litter size, mate finding, pollen limitation, juvenile survival, predator dilution). Demographic Allee effects are defined as the positive relationship between population density and the collective component Allee effects (overall individual fitness). A demographic Allee effect is comprised of one or more component Allee effects (Stephens et al. 1999; Courchamp et al. 2008).

Demographic Allee effects can also be classified as weak or strong Allee effects dependent upon an Allee threshold being present (strong) or not (weak) (Stephens et al. 1999). Strong Allee effects represent populations in which per capita growth rate becomes negative below a threshold. Weak Allee effects represent populations whose per capita growth slows down at lower densities but stays positive (Courchamp et al. 2008). Populations with a strong Allee effect are generally easier to detect than a weak Allee effect and sufficient growth rate and time series data is essential to recognize an Allee threshold (Johnson et al. 2006; Courchamp et al. 2008).

Allee effects are an important concept in conservation biology because conservation biology typically deals with small and declining populations (Stephens and Sutherland 1999). Important issues in conservation biology include habitat fragmentation, poaching and anthropogenic encroachment. Although

these issues are not Allee effects themselves, they can push a population with a strong Allee effect towards quicker extinction (Courchamp et al. 2008). Conservationists are also concerned with reinforcing (human aided propagule release) declining populations and thus need to understand whether a species has an Allee effect. Threatened populations with Allee effects require more propagules to be initially released to ensure recovery than populations with no or very weak Allee effects (Courchamp et al. 2008).

On the other end of the spectrum, invasion ecologists are starting to consider Allee effects an important concept in why some invading species are more successful than others (Taylor and Hastings 2005; Drake and Lodge 2006; Berec et al. 2007; Liebhold and Tobin 2008; Courchamp et al. 2008; Tobin et al. 2011). Invading organisms are typically comprised of small founder populations that are exposed to new environments and most do not become established and persist in the environment (Leung et al. 2004; Petrovskii et al. 2005; Lockwood et al. 2005; Tobin et al. 2011; Brockerhoff et al. 2014). The rate that established populations can spread through a landscape is also limited by Allee effects (Lewis and Kareiva 1991). Exotic organisms that are able to establish provide ecologists with a set of biological traits and characteristics beneficial to overcoming stochastic conditions and Allee thresholds (assuming one exists in the first place). With this information, ecologists and biosecurity managers are able to create databases highlighting species and groups of organisms that are likely to be transported and successfully invade a new environment (Drake and Lodge 2006; Brockerhoff et al. 2014).

Biosecurity and invasive alien species

Invasive alien species are the second greatest threat to biodiversity globally following habitat loss (Bax et al. 2003; Clavero and Garcia-Berthou 2005) and can adversely affect ecosystem functions and services (Luque et al. 2013; Simberloff et al. 2013). Invasive species are also economically costly. Approximately $300 billion is spent or lost each year globally and the costs are typically not covered by the companies associated with the invasion events (Pimentel et al. 2005; Perrings et al. 2002; Genovesi 2011). The likelihood of invasive species entering new environments is increasing with the intensification of global trade (Jenkins 1996; Perrings et al. 2002; Levine and D'Antonio 2003; Perrings et al. 2005; Brockerhoff et al. 2006a; Hulme 2009; Perrings et al. 2010; Marini et al. 2011).

Biosecurity, the protection of a country from biological impacts (Perrings et al. 2005), is increasingly important to prevent new biological invasions from occurring. Unfortunately, a conflict exists between the goals of an individual country's biosecurity efforts and global economic goals because there is no way to make international traders pay for potential impacts of invasive species (Perrings et al. 2005; Perrings et al. 2010). It has been suggested that the best solution is to internalize the costs by incorporating a "polluter pays principle" and to make these costs an international rather than a national effort (Brasier 2005; Perrings et al. 2005; Brasier 2008; Perrings et al. 2010). Until the World Trade Organization (WTO) encourages individual countries to internalize these costs, nations and individual landowners are left to

absorb the economic and ecological costs caused by invasive species (Perrings et al. 2005; Aukema et al. 2011; Liebhold et al. 2012).

Biosecurity strategies currently in place to identify or control new invasive pests include: (1) compiling risk assessment databases of harmful or potentially harmful organisms (Pheloung et al. 1999; Brazier 2008), (2) quarantine precautions (based on risk assessments) (Hewitt and Campbell 2007), (3) visual inspection techniques (Brazier 2008) and (4) early detection and rapid response (EDRR) procedures (Meyerson and Reaser 2002). Biosecurity tools include: (1) DNA barcoding (Hebert et al. 2003; Armstrong and Ball 2005; Collins et al. 2012; McCarthy et al. 2013a), (2) physiological inducement strategies (e.g., using the marine yeast *Rhodosporidium paludigenum* to combat fruit pathogens) (Wang et al. 2014), and (3) pheromone baited insect traps (Brockerhoff et al. 2006b; Rassati et al. 2015). Although these measures are in place, biosecurity offices at ports of entries are typically understaffed and only a small portion of goods are inspected (e.g., The Animal and Plant Health Inspection Services [APHIS] in the USA estimates they inspect ~2% of imported plant stock) (Brazier 2008).

Major invasion pathways such as ship ballast water, the ornamental live plant trade, the timber trade industry and solid wood packaging materials are moving organisms around the world at unprecedented levels (Allen and Humble 2002; Brazier 2008; Hulme 2009; Skarpass and Økland 2009; Butchart et al. 2010; Eschen et al. 2015). In this thesis, I will focus on a group of organisms commonly transported in solid wood packaging materials and the timber trade: bark beetles, one of the most commonly intercepted and economically important group of insects intercepted at ports of entry around the world (Holmes et al. 2009; Koch et al. 2010; Haack 2011; Grégoire et al. 2015).

The stepwise process of a biological invasion is arrival, establishment, integration and spread (Vermeij 1996; Blackburn et al. 2011). Arrival is simply the dispersal, either natural or human-assisted (also called extra-range dispersal [Wilson et al. 2009]), of an organism to an un-occupied area. Establishment occurs when enough propagules arrive in a suitable habitat and extinction becomes unlikely (Memmot et al. 1998; Berggren 2001; Keitt et al. 2001; Lockwood et al. 2005; Colautti et al. 2006). The quality (or physiological well-being) of arriving propagules also influence establishment success and reproduction output of invading populations (Lange and Marshall 2016). Integration is how the resident organismal community ecologically and evolutionarily responds and interacts with the newly established invader (Vermeij 1996). Spread is the expansion of the invader's range into new areas, where the stepwise process of arrival and establishment is repeated across space and time. In this study, I focused on the population dynamics of invading bark beetles (Coleoptera: Scolytinae) during the initial establishment phase.

Bark beetles

Bark beetles (Coleoptera: Scolytinae) are a numerous and diverse group of insects with more than 6,000 species across 247 genera worldwide (Wood 1982a; Kirkendall et al. 2015). Bark beetles are insects that can exploit coniferous and deciduous trees, fruit trees, ornamental trees, vines and shrubs. Bark beetles can be found in almost any climate and habitat where woody plants and forest trees are able to grow (Berryman et al. 1984). Services provided by bark beetles include nutrient cycling, food for wildlife and maintaining forest structure, composition and stability (Kirkendall 1983; Berryman et al. 1984; Haberkern and Raffa 2003; Raffa et al. 2008). Additionally, a few bark beetles are important forest pests that cause tremendous changes to forests on a landscape scale (Christiansen et al. 1987; Raffa et al. 2008).

Three life history strategies are used to describe bark beetles: primary, secondary and saprophytic (Raffa et al. 1993; Paine et al. 1997). Primary bark beetles colonize and feed on healthy trees (Coulson 1979; Paine et al. 1997; Haberkern and Raffa 2003). Mass aggregations, driven by sex pheromone response, of primary bark beetles can result in tree mortality (Renwick and Vité 1972; Coulson 1979; Wood 1982b). Populations of primary bark beetles fluctuate from low to high and are able to congregate in lower to higher vigor trees respectively (Berryman et al. 1976; Paine et al. 1984). Secondary bark beetles colonize stressed, damaged and recently dead trees and also utilize sex pheromones to locate each other (Paine et al. 1997). Trees initially killed by primary bark beetles are often colonized by secondary bark beetles (Borden et al. 1992). Outbreaks of secondary bark beetles are rare. However, in rare occasions, if large quantities of host resource (damaged trees) accumulates from anthropogenic or environmental disturbances, populations can build large enough to overcome healthy tree defenses (Paine et al. 1997; Hayes et al. 2008). Saprophytic bark beetles colonize dead hosts and are the most common and species numerous of the three groups (Paine et al. 1997). Because saprophytic beetles are very rarely considered economic pests, this group is probably the least studied. This is unfortunate because some saprophytic bark beetles that have mutualistic relationships with *Ophiostoma* and *Leptographium* fungi have spread outside their native range and become important pests (Harrington et al. 1993; Paine et al. 1997). Some authors lump saprophytic and secondary bark beetles together (Paine et al. 1997). I do not follow this approach because the differing life history strategies and pheromone dependency of secondary bark beetles have important implications for predicting the invasiveness of each group. Understanding the life history strategies of bark beetles is important in identifying the most likely species to cause ecological and economic harm if established in regions outside of their native range.

Bark beetles have been distributed all over the world via human mediated transportation (Paine et al. 1997; Marini et al. 2011). Fifty species of exotic bark beetles are known to have established in the United States (Haack 2001) and 11 species are established in the island nation of New Zealand (Brockerhoff et al. 2003), with many more species being intercepted in both nations. The immature stages of bark beetles (and other bark and wood boring insects) live underneath bark and between the xylem and

phloem and can be moved in timber or solid wood packaging materials. Therefore, visual detection of these organisms is difficult. Fortunately, to minimize the number of insects transported around the world, phytosanitary standards have been introduced by the International Plant Protection Convention (IPPC) (see the International Standards for Phytosanitary Measures [ISPM] 15 guidelines). These standards require all wood packaging material greater than 6 mm in thickness to be debarked and either heat treated at a core temperature of 56° C for at least 30 minutes or receive a treatment of methyl bromide over a period of 24 hours at 10° C from countries of concern (Britton and Liebhold 2013; Haack et al. 2014). As the global economy continues to expand both in commodities shipped and countries commodities are shipped from, the number of bark beetles and other non-native organisms are also expected to increase (Marini et al. 2011; Eschen et al. 2014).

Study species in New Zealand and the United States

Hylastes ater Paykull and *Hylurgus ligniperda* F. (Fig. 1.1) are two saprophytic bark beetles that arrived in New Zealand before the implementation of the standards (ISPM 15) set by the International Plant Protection Convention. *Hylastes ater*, native to Europe, was first detected in New Zealand circa 1929 (Clark 1932) and is now widespread through the North and South Islands. *Hylastes ater* is not typically considered a forest pest, however, it has recently been found to attack and kill some saplings in radiata pine (*Pinus radiata*) plantations (Reay et al. 2012). *Hylurgus ligniperda*, native to Eurasia, was first detected in New Zealand circa 1974 (Bain 1977) and is now widespread through the North and South Island. Both *H. ligniperda* and *H. ater* have a symbiotic relationship with Ophiostomatoid fungi and are considered important quarantine pests, meaning that management costs are associated with exporting all timber in order to prevent these beetles from becoming established in a new environment (Reay et al. 2005; Reay et al. 2006a, b; McCarthy et al 2013b).

Figure 1.1 – The two saprophytic bark beetles investigated in this thesis, *Hylurgus ligniperda* (left) and *Hylastes ater* (right).

Ips pini Say (Fig. 1.2) is a secondary bark beetle native to North America that utilizes multiple species of *Pinus*. Two distinct sub-populations of *Ips pini* exist in eastern and western North America that are separated by different enantiomers of the sex pheromone Ipsdienol (Lanier et al. 1980; Miller et al. 1989; Erbilgin 2003). *Ips pini* populations typically exist in a non-tree killing stable state dependent on habitat quality and natural predators (Erbilgin et al. 2002). However, increased breeding material, such as trees stressed by pathogens and root feeding insects (Klepzig et al. 1991; Erbilgin and Raffa 2002), sometimes allow local populations to overcome healthier tree defenses and enter an outbreak phase for a short time period (Schenk and Benjamin 1969). *Ips pini* has been intercepted 6 different times in New Zealand but has not become established (Brockerhoff et al. 2003). A closely related species, *Ips grandicollis* Eichhoff, is also a secondary bark beetle that rarely kills pine trees in North America. However, *I. grandicollis* has become established in Australia where it has caused heavy tree mortality and is now considered a major pine plantation pest (Morgan 1967, Neumann and Morey 1984, Neumann 1987, Stone and Simpson 1987). Fear exists that if *I. pini* was to establish outside of its native range and escape the competitive and predatory forces that keep its populations in check, outbreaks could occur causing widespread stand mortality. *Ips typographus* (a primary bark beetle) is the largest killer of spruce forests in Europe (Grégoire and Evans 2004), and in New Zealand and the United States it is 1 of the 5 most commonly intercepted species (Brockerhoff et al. 2006b), yet it has never become established outside of its native range. Identifying the life history traits of bark beetles that promote or deter successful establishment can help inform what characteristics could be exploited to reduce invasion likelihood.

Figure 1.2 – The secondary bark beetle investigated in this thesis, *Ips pini*

Research objectives and hypothesis

The objective of this thesis was to better understand what role Allee effects play in determining the invasion success of bark beetle founding populations during the arrival and spread phases. Specifically, I asked the following two questions:

1 - *How does dispersal ability influence species range expansion in the face of an Allee threshold?*

2 - *Can a demographic Allee effect prevent population establishment of small founder populations during the arrival phase of invasion?*

In order to carry out empirical releases of bark beetles to determine their Allee thresholds, the first step was to find areas where natural background populations did not exist. This turned out to be much harder than one might think, even at great distances away from host resources. It could even be said that almost everywhere I looked for bark beetles, I found them! Thus, the dispersal capabilities and spread of bark beetles through fragmented landscapes on a large scale became a major focus of this thesis and are presented in Chapters 2 (*H. ater* and *H. ligniperda*) and Chapter 3 (*I. pini*). Nonetheless, I did find areas with either very low or no bark beetles present in New Zealand and the United States and was able to investigate the role of Allee effects during simulated invasion events of *H. ligniperda* and *I. pini* (Chapter 4). I conclude the thesis in chapter 5 by synthesizing and applying what I have learned to different fields of ecology and how it can be applied to managing and preventing future invasions of bark beetles.

Chapter 2 - Long distance dispersal of non-native pine bark beetles from host resources

Introduction

Which traits make wood and bark boring beetles (Coleoptera: Scolytinae) one of the most successful groups of biological invaders? In addition to high propagule pressure (Brockerhoff et al. 2014), good dispersal ability, effective host detection and the availability of host resources are also clearly associated with colonization success (Byers 1996; Skarpaas and Økland 2009). Bark and ambrosia beetles can be accidentally transported in logs shipped overseas or in wooden pallets, crates and dunnage (Brockerhoff et al. 2006a; Piel et al. 2008; Liebhold et al. 2012). Following transport, emerging populations may establish, potentially causing major ecological and economic damage on forest ecosystems and plantation forestry (e.g., *Ips grandicollis*, *Dendroctonus valens*, *Xyleborus glabratus*) (Morgan 1967; Yan et al. 2005; Fraedrich et al. 2008). Following establishment, populations may subsequently expand their range into regions with suitable habitat; this spread occurs as a combined result of both population growth and dispersal (Skellam 1951; Williamson 1996; Liebhold and Tobin 2008).

While the majority of spreading insect populations typically disperse relatively short distances, a small fraction may disperse very long distances, either passively (e.g., anthropogenic transport), actively (e.g., flying), or semi-passively (e.g., an actively flying insect carried by wind), to novel habitat locations (Coulson et al. 1979; Shigesada et al. 1995; Suarez et al. 2001; Liebhold and Tobin 2008). Consequences of such a "fat-tailed" dispersal kernel can include increased rates of range expansion, dampened inbreeding depression, escape from predators and parasitoids, and reduced intra-specific competition (Dytham 2009). Risks and costs associated with long distance dispersal include arrival at locations with low quality habitat (or unsuitable habitat) or dispersal beyond the climatic limit of the species (Dytham 2009, Bonte et al. 2012). Additionally, low numbers of colonizing propagules are subject to Allee effects (inverse density dependence), potentially resulting in establishment failure and slower spread (Kot et al. 1996; Keitt et al. 2001; Taylor and Hastings 2005).

The ability of a dispersing organism to detect a suitable host is a critical component of successful establishment (Moeck et al. 1981). Some colonizing bark beetles respond positively to primary attractants (volatile organic host compounds including resins, alcohols and terpenes) released by senescing or damaged trees (Person 1931; Moeck et al. 1981; Raffa et al. 1983; Borden 1989; Miller 2006). In some bark beetle species, pioneer beetles produce aggregation pheromones that attract conspecifics, sometimes causing mass-aggregation on hosts that allow the beetles to overcome host

defenses (Wood 1982; Raffa and Berryman 1983). At close range, visual cues may also become important in host detection by colonizing bark beetles (Wood 1972; Hynum and Berryman 1980; Saint-Germain et al. 2007). Additionally, the size and spatial arrangement of patches in a landscape can positively or negatively shape occupancy probabilities of organisms with different immigration and emigration behaviors (Bowman et al. 2002; Englund and Hambäck 2007; Sahlin and Schroeder 2010). The dispersal success and distribution of bark beetles (and organisms in general) is defined by multiple processes interacting simultaneously.

The goal of this study was to determine how far invading bark beetles disperse from host material in a fragmented landscape, to improve our understanding of dispersal dynamics during biological invasions. Specifically, I investigated the dispersal capabilities and abundance of two non-native bark beetles in relation to pine plantations and pine shelterbelts in remote regions of New Zealand. I also related abundance to spatially weighted estimates of pine density.

Methods and materials

Study system

Hylastes ater Paykull and *Hylurgus ligniperda* F., both native to Eurasia, are two of the world's most successful bark beetle colonizers and have established in many Southern Hemisphere countries with pine plantations (Brockerhoff et al. 2006a). Although neither species kills living trees, as they are saprophytic insects (dead wood infesting), both species are facilitators of the infestation and spread of timber-degrading ophiostomatoid fungi in the genera *Ophiostoma* and *Leptographium* (McCarthy et al. 2013). *Hylastes ater* was detected in New Zealand in 1929 (Clark 1932) and *H. ligniperda* in 1974 (Bain 1977). Since their introduction, both species have spread to most pine plantations throughout both the North and South Islands of New Zealand.

In New Zealand, there are no native species in the family Pinaceae; however, many species have been introduced for ornamental and timber production purposes, and 18 species have become naturalized (Webb et al. 1988). Non-native plantation forests (including *Pinus* spp. and Douglas fir *Pseudotsuga menziesii*) cover ~1.7 Mha and are a major component of the New Zealand economy (NZFOA 2014). Unfortunately, wilding pine and Douglas fir trees have become important invaders in New Zealand covering at least 500,000 ha in the South Island alone (Ledgard 2001; Gous et al. 2014). Many wilding conifer stands are young and vigorous with little dead wood and thus should not currently provide suitable host material for *H. ater* and *H. ligniperda* to breed in. However, as these stands mature or trees are killed to limit the spread of wilding conifers, the stands could provide suitable bark beetle host material.

Trapping network

To sample dispersing *H. ater* and *H. ligniperda*, I deployed 169 traps across 12 study areas (11 areas in the Southern Alps and one area on Stewart Island) and 10 control (likely beetle-source) areas (five pine plantations, two wilding pine areas, and three pine shelterbelts) throughout the South Island of New Zealand from October 2012 – March 2013 (Fig. 2.1, Table 2.1). Study areas were selected to vary in distance and isolation from operational pine plantations, including several areas located in remote valleys entirely vegetated by grasslands and surrounded by mountains with native vegetation devoid of any pine trees. In all study areas, I recorded the dominant vegetation type (obtained from the Landcare LRIS portal, Land Cover Database v4.0 [Informatics Team Landcare Research 2015]) within each valley (Table 2.1).

Traps consisted of black panel insect traps (Kerr 2010) baited with the host (*Pinus* spp.) primary attractants α-pinene (release rate of ca. 0.02 g/day) and ethanol (release rate of ca. 0.76 g/day); currently no secondary semiochemicals (i.e., sex pheromones) are known from either species (Perttunen 1957; Reay and Walsh 2002; Petrice et al. 2004; Brockerhoff et al. 2006b). Lures consisted of attractant baits packaged as 150 ml of each attractant in sealed polyethylene bags. All panel traps were hung from metal fence posts (~ 1.5 m) deployed in pairs separated by ~ 0.5 km and located along transects with at least 3 km between pairs (mapped using a handheld GPS). The length of each transect and number of trap pairs varied with the length of the study area. Each pine shelterbelt area (N = 3) contained one pair of traps and both wilding pine areas contained two pairs of traps. Traps were placed in plantation forests to serve as high-beetle-density reference sites. The number of traps placed in pine plantations varied from two to four traps. Traps placed in Ashley forest (a pine plantation) were part of a national forest insect survey program (Pawson 2015, unpublished data). The two traps from the Oxford plantation forest were not included in the analysis because they were filled with pine needles at every trap check, which prevented bark beetles from entering and/or allowed them to escape. Sampling periods varied from 89 days (Stewart Island) to 218 days (Wilberforce and Avoca; Table 2.1), according to local weather conditions and other limitations on site access.

The identity of *Hylastes ater* adult samples trapped on Stewart Island were confirmed by John Bain (New Zealand Forest Research Institute/Scion) and specimens deposited in the National Forest Insect Collection at the New Zealand Forest Research Institute, Rotorua, as this was the first record of this species on Stewart Island.

Distance measurements

Distance from individual traps to the nearest operational pine plantation were measured in ArcMap (version V 10.1, ESRI 2011) using the New Zealand mainland exotic vegetation layer imported from the Landcare LRIS portal, Land Cover Database v4.0. A straight-line distance was drawn from the

edge of the nearest pine plantation to the center point of the trap pair to obtain distance. I defined an operational pine plantation as a forest that has been harvested within ~2 years of trapping, to ensure that suitable breeding habitat was available in the form of slash and stumps.

Although I expected most bark beetles captured to originate from pine plantations containing large amounts of continuous host material (stumps and dead woody material in contact with the ground), it is possible that dead pine tree material in fragmented agricultural landscapes with shelterbelts and small stands of pines also provide host material for small populations to persist. Therefore, I also measured distance from individual traps to the nearest pine shelterbelt. Distances were individually measured in Google Earth (Version 7.1.5.1557) because the Land Cover Database layer does not show all shelterbelts. Distance measurements were taken from Google Earth satellite imagery dated 29 September 2013. I defined a shelterbelt as a continuous stretch of *Pinus* spp. at least 25 m in length except for Stewart Island where a small private plantation of *Pinus* spp. was used for the analysis, as it is the only continuous patch of *Pinus* spp. on the island. It is important to note that, although relatively uncommon, smaller shelterbelts and individual pines that I did not include in my analysis do exist across the mid-Canterbury landscape which may provide suitable host material for *H. ater* (see Appendix B). In New Zealand, many wilding pine areas are young and vigorous stands (i.e., without breeding material such as deadwood and therefore unsuitable habitat) and hence were not considered as relevant breeding material in the analysis. A straight-line distance was measured from the trap to the edge of the nearest pine shelterbelt.

Inverse distance weighted estimates

To quantify the effect of local pine density on bark beetle capture, I calculated inverse-distance weighted average estimates of pine densities around each trap. Data on pine densities were extracted from a national (New Zealand) vector GIS layer of pine forest cover (Informatics Team Landcare Research 2015). This coverage was converted into a 1 km raster layer with each raster cell coded as the proportion of the cell covered by pine forests. This vector to raster conversion was performed using ArcGIS software (ESRI 2011).

Two matrices (c and d) were used to delineate a fixed neighborhood of pine density and distance from a focal point (insect trap) (Liebhold et al. 1993). The first matrix, *c*, contained 1 km × 1 km cells with values of conifer density based on the New Zealand mainland exotic raster layer used previously for straight-line distances. Note that the original vector coverage actually corresponded to all conifers and I could not separate Douglas fir (*Pseudotsuga menziesii*) from *Pinus* species. However, the area of Douglas fir was small so the density estimates should be dominated by pines.

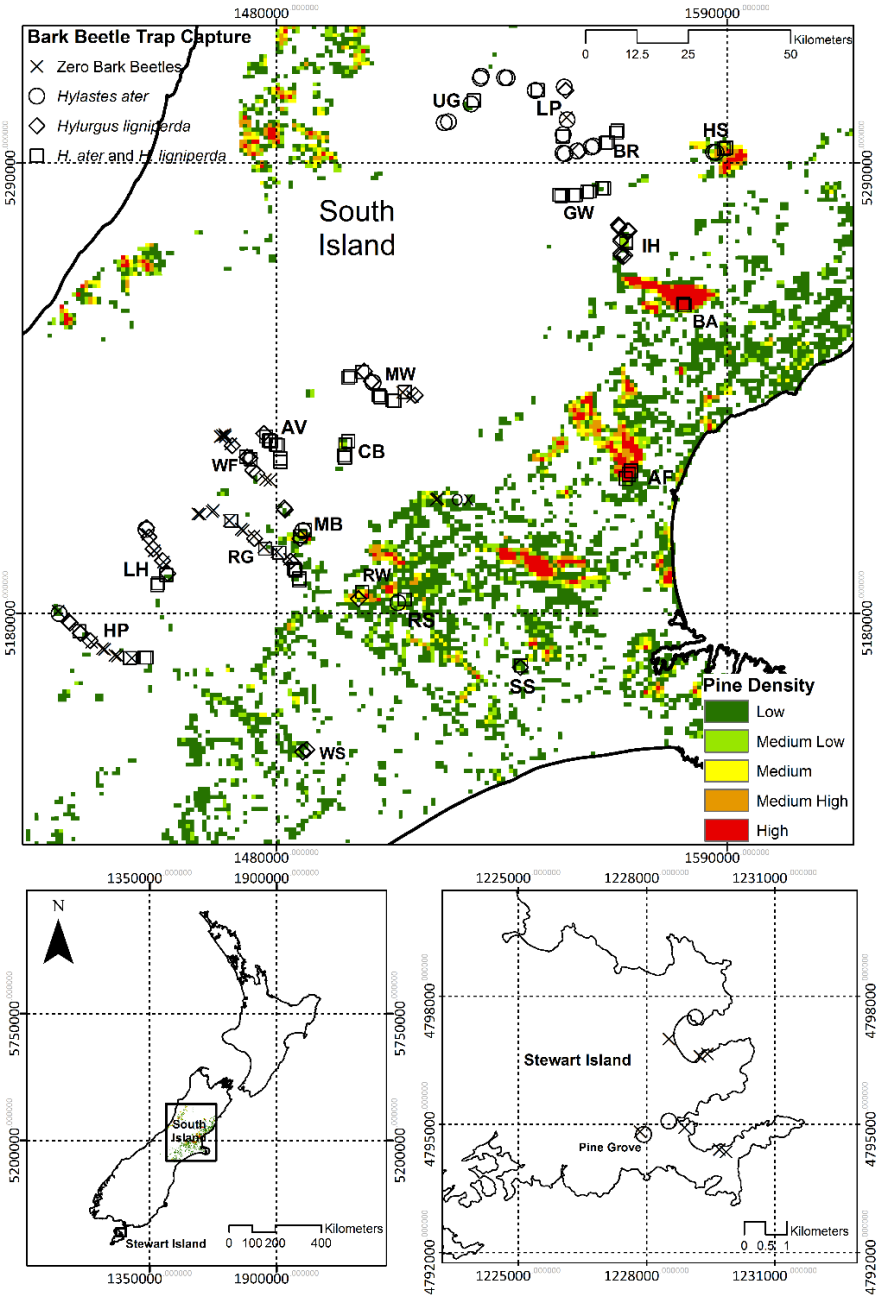

Figure 2.1 - Location of the 156 panel traps in the Southern Alps and 10 panel traps in Stewart Island, and local density of pines derived from the Landcare LRIS portal, Land Cover Database v4.0. Refer to Table 2.1 for categorization of study and control sites and for codes to site names. White pixels on land represent zero pine density.

Table 2.1 - Site characteristics and trapping results across South Island and Stewart Island. Two letter codes can be used to identify sites in Fig. 2.1.

Site	Vegetation Type	# Traps	Trapping period (month/year)	# Trap days	Nearest pine plantation (~km)[1]	*Hylurgus ligniperda*/trap/week	*Hylastes ater*/trap/week
Ashley Forest (AF)	Exotic Forest	3	10/13 – 4/14	188	0	75.05	2.45
Balmoral Forest (BF)	Exotic Forest	2	10/13 – 4/14	149	0	3.68	0.43
Rockwood Forest (RW)	Exotic Forest	2	10/13 – 1/14	181	0	3.17	0.02
Hanmer Springs Forest (HS)	Exotic Forest	4	11/13 – 4/14	144	0	0.72	0.57
Oxford Forest (OX)	Exotic Forest	2	10/13 – 4/14	181	0	0.00	0.00
Selwyn Shelterbelt (SS)	Exotic Forest, exotic grassland	2	10/13 – 4/14	181	23	0.40	0.04
Westerfield Shelterbelt (WS)	Exotic Forest, exotic grassland	2	10/13 – 4/14	181	27	0.04	0.00
Rockwood Shelterbelt (RS)	Exotic Forest, exotic grassland	2	10/13 – 4/14	181	2	0.02	0.04
Cragieburn Wilding Pine (CB)	Exotic Forest, exotic grassland	4	9/13 – 4/14	202	1	0.77	0.75
Mt. Barker Wilding Pine (MB)	Exotic Forest, exotic grassland	4	9/13 – 4/14	218	16	0.16	0.05
Island Hills (IH)	Exotic grassland, exotic forest, kanuka and manuka forest	12	11/13 – 2/14	103	0	7.15	0.05
Mt. White (MW)	Exotic grassland and grey scrub	14	9/13 – 4/14	202	13	0.29	0.74
Glynn Wye (GW)	Exotic grassland and exotic forest	8	11/13 – 3/14	144	15	0.47	0.54
Avoca River (AV)	Exotic and tussock grassland, grey scrub	10	9/13 – 4/14	218	18	0.20	0.07
Wilberforce River (AV)	Exotic grassland and grey scrub	14	9/13 – 4/14	218	22	0.0005	0.00
Rakaia River (RG)	Exotic grassland	20	9/13 – 4/14	188	24	0.09	0.06
Boyle River (BR)	Exotic grassland	10	11/13 – 3/14	134	25	0.2	0.27
Upper Grey (UG)	Indigenous forest and exotic grassland	6	12/13 – 3/14	106	29	0.03	5.66

Haketere (HP)	Exotic and tussock grassland	16	11/13 – 4/14	132	33	0.07	0.08
Lake Heron (LH)	Herbaceous freshwater vegetation, grey scrub and exotic grassland	12	9/13 – 4/14	199	34	0.18	0.03
Lewis Pass (LP)	Exotic grassland	10	12/13 – 3/14	132	40	0.03	0.2
Stewart Island	Indigenous forest and broadleaved indigenous hardwoods	10	1/14 – 4/14	89	40	0.00	0.09

The second matrix, *d*, was created using a distance decay function (Euclidean distance):

Equation 2.1 $$\sqrt{((xlim + 1) - x_i)^2 + ((ylim + 1) - y_i)^2}$$

where xlim and ylim sets a maximum extent of the *c* matrix included to obtain estimates from the focal point x_i and y_i. The maximum extent used was 50 km (i.e., 50 × 50 cells) because this distance would include at least 1 operational pine plantation for all traps and I observed bark beetles at least 40 km from any pine plantation (Table 2.1). Furthermore, because of the nature of the inverse distance weighting function, points more distant than 50 km would have a negligible effect on estimates.

Spatially weighted average pine density *w* around each trap was computed from all raster cells within 50 km of each trap location using an inverse distance power weight function,

Equation 2.2 $$w = \frac{\Sigma \frac{x_i}{d_i^p}}{\Sigma \frac{1}{d_i^p}}$$

where *p* = a power parameter that was varied to obtain the best fit in the regression of trap capture on weighted pine density. The inverse density function gives greater weight to nearby locations, but the parameter *p* determines the rate at which the distant areas decrease in their contribution to the estimate. Specifically, if the best-fit model had a low value of *p* (e.g., 0.5), beetle catch was affected by even quite remote pine stands, implying that dispersal was effective over long distances, whereas if the best fit model had a high value of *p* (e.g., 3.0), beetle catch was affected mainly by local sources, implying limited long-distance dispersal (see Lu and Wong 2008). I tested models with a *p* value of 0.1, 0.5, 1, 1.5, 2, 2.5 and 3 and used the best-fit value of *p* for all subsequent analyses for that species. Weighted average pine densities were computed using a script written in the R language (V. 3.2.3, R Development Core Team 2015, Appendix A).

Statistical analysis

Counts (bark beetle trap^{-1}; N = 167 traps) of *H. ligniperda* and *H. ater* were analyzed using negative binomial generalized linear models with a log link in the statistical software R version 3.2.3 (R Development Core Team, 2015; R package MASS, Venables and Ripley 2002). Negative binomial models were used to account for overdispersion and to allow model comparisons based on the Akaike Information Criterion (AIC) (Akaike 1973). I did not run models with combinations of weighted average pine density, *w,* as these values would be highly autocorrelated because of the nested structure of the data. Potential outliers that could cause confounding effects on regression models were checked using Cook's distance considering a value of 1 as threshold (Fox 2002) but no influential outliers were found. Likelihood ratio tests were used to assess the significance of the fixed term(s) in each regression model

(drop1 command in R, Zuur et al. 2009). For each model, I also calculated the explained deviance, also known as pseudo R^2, following Dobson (2002).

Four models were run for each species containing the following predictors: 1) distance to the nearest pine plantation; 2) distance to nearest pine shelterbelt; 3) weighted estimate of pine density using best-fit value of *p* as described above; 4) a multiple regression including distance to plantation, distance to shelterbelt, and weighted pine density estimate. I used an offset function in all models to account for the variation in number of trapping exposure days (Zuur et al. 2009).

Results

Pine distance and density effect on Hylurgus ligniperda

I captured 4900 *H. ligniperda* (84% of all captured) in pine plantations. As expected, the highest trap catch of *H. ligniperda* occurred in a pine plantation (Ashley Forest, mean = 75.5 $trap^{-1}$ $week^{-1}$). For traps away from plantations, I captured 844 *H. ligniperda* across all 11 sites in the Southern Alps, but none on Stewart Island (Table 2.1). A total of 23 and 112 *H. ligniperda* were captured across the shelterbelt and wilding pine sites, respectively. The most remote location at which *H. ligniperda* was captured was 40.4 km from the nearest pine plantation and 26.3 km from the nearest pine shelterbelt.

Hylurgus ligniperda trap capture significantly decreased with increasing distance to pine resources in all modeled scenarios (Fig. 2.2 and 2.3). *Hylurgus ligniperda* abundance was negatively correlated with distance to pine plantation (L = likelihood ratio test statistic; L = 229.31, df = 1, P = < 0.001, deviance explained = 58%) and distance to pine shelterbelt (L = 34.77, df = 1, P = < 0.001, deviance explained = 17%; Fig. 2.2). The best distance power function for weighted pine density for *H. ligniperda* was p = 0.5 (AIC = 861.3, next lowest AIC = 866.51 [p = 0.1]), meaning that distant pines still make important contributions to local catch rates, i.e., that dispersal is effective. Using this value of *p*, *H. ligniperda* catch was significantly negatively related to pine density w (L = 260.52, df = 1, P = <0.001, deviance explained = 61%; Fig. 2.3a). The multiple regression model which included distance to plantation, distance to shelterbelt, and weighted density was the best predictor of *H. ligniperda* (i.e., the model with the highest explained deviance) showing that all three different estimates of pine resources made independent contributions to predicted catches (Table 2.2).

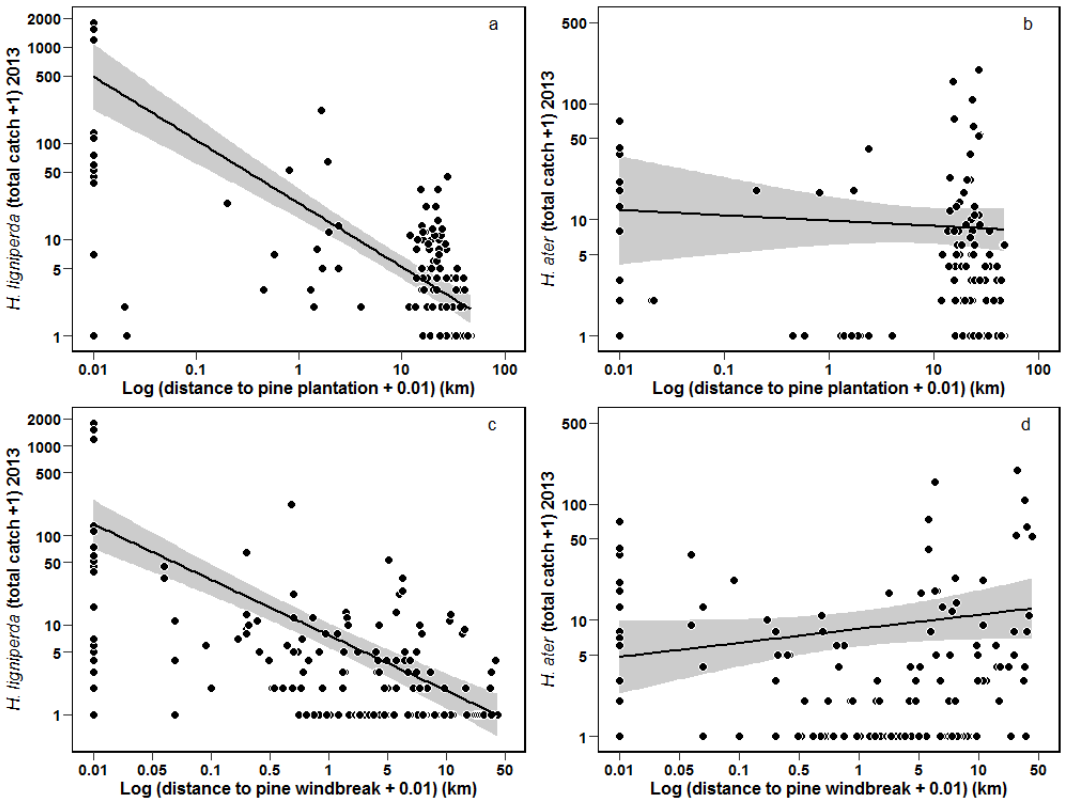

Figure 2.2 - Trap captures of *H. ligniperda* (a, c) and *H. ater* (b, c) as a function of distance to the nearest pine plantation (a, b) or shelterbelt (c, d). Lines represent significant negative binomial generalized linear model fits; grey areas indicate 95% confidence intervals. N=167 traps.

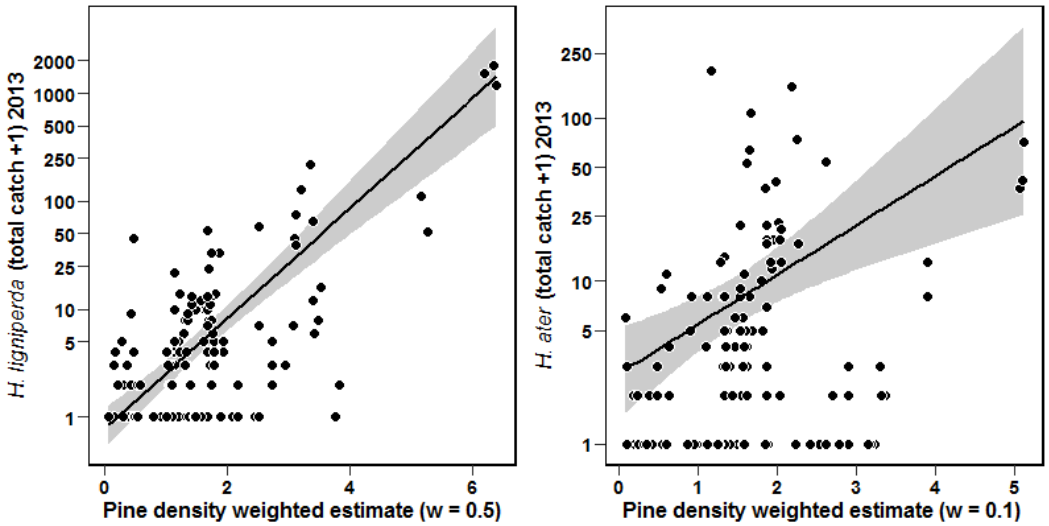

Figure 2.3 - Total beetle catch per trap as a function of pine density weighted estimate for (left) *H. ligniperda* and (right) *H. ater*. Lines represent significant negative binomial generalized linear model fits using weighted pine density, calculated using the best-fit power scaling function *p* given on the x-axis. Grey areas indicate 95% confidence intervals. Note differences in y-axis values.

Pine distance and density effects on Hylastes ater

I captured 217 *H. ater* in pine plantations. Unexpectedly, more *H. ater* were captured at non-plantation sites (Upper Grey Valley: 37% of total capture, mean = 5.7 trap^{-1} week^{-1}, Mount White Station: 31% of total capture) than in pine plantations (17% of total capture). A total of 1059 *H. ater* were captured across the twelve non-plantation study sites in the Southern Alps and on Stewart Island. *Hylastes ater* was captured at all 12 sites apart from Wilberforce (Table 2.1), including on Stewart Island (this is the first known record of *H. ater* on Stewart Island). A total of four *H. ater* were captured across the three shelterbelt sites in the Canterbury plains. At the wilding pine sites, 97 *H. ater* were captured. The most distant captures of *H. ater* occurred 43.0 km from the nearest pine plantation and 27.6 km from the nearest pine shelterbelt.

Hylastes ater abundance was not correlated with trap distance from the nearest pine plantation (L = 2.49, df = 1 P = 0.11, deviance explained = 2%). Unexpectedly, trap catch was significantly *positively* correlated with increasing distance to the nearest pine shelterbelt (L = 23.95, df =, P = < 0.001, deviance explained = 64%) (Fig. 2.2). The best fit power function for *Hylastes ater* abundance in relation to pine density occurred at p = 0.1 (AIC = 853.09, next lowest AIC = 847.23 [p = 0.5]), a very low value indicating that catches were affected strongly by even distant pine stands. Relatively high numbers of *H. ater* were observed at the highest values of pine density w but the highest abundances occurred at intermediate values

of pine density (L = 8.65, df = 1, P = 0.003, deviance explained = 5%; Fig. 2.3b). The multiple regression model including distance to plantation, distance to shelterbelt, and weighted pine density w was the best fit model overall, showing that for *H. ater* these three different measures of pine resource all contributed to predicted trap catch rates (Table 2.2).

Table 2.2 - Multiple regression negative binomial GLM output from the drop1 function in R predicting bark beetle trap capture across all sites, 2013-2014, predicted from distance to nearest plantation, distance to nearest shelterbelt, and weighted pine density (w). Weighted density was calculated using best-fit estimates for power function p (0.5 for *H. ligniperda*, 0.1 for *H. ater*), see text.

Bark Beetle	Predictor	d.f.	Deviance	LRT	Pr (>Chi)	Deviance explained
Hylurgus ligniperda	Null		167.12			67%
	Distance Plantation	1	184.5	17.38	<0.001	
	Distance Shelterbelt	1	177.31	10.19	0.001	
	Weighted density	1	194.14	27.04	<0.001	
Hylastes ater	Null		158.85			26%
	Distance Plantation	1	162.61	3.75	0.05	
	Distance Shelterbelt	1	194.29	35.44	<0.001	
	Weighted density	1	163.66	4.81	0.03	

Discussion

The Eurasian bark beetles *Hylastes ater* and *Hylurgus ligniperda* are invasive pests that have successfully colonized most pine growing countries in the Southern Hemisphere. Our results show that one contributing factor to their invasion success could be their effective long distance dispersal, even across a heavily fragmented landscape, as indicated by their abundance as a function of host availability. The very low values for the spatial scaling function p, and trap captures tens of kilometers from the nearest pine resources all indicate surprisingly high levels of long distance dispersal in these two bark beetles. Overall, our study provides new insight into traits positively associated with the spread and establishment of two non-native bark beetles and has wider implications for bark beetle ecology and biological invasions.

At the start of this study, I expected to find remote areas distant from pine resources to be absent of *H. ater* and *H. ligniperda*. Yet, this was not the case. Instead, I captured both bark beetles in almost every area I looked, often on more than one occasion throughout the flight season. The observed dependence of trap catch rates on distance from host material (i.e., pine resources) differed markedly between the two bark beetles. Trap catch rate of *H. ligniperda* was closely associated with higher values of pine density (i.e., pine plantations) whereas clustering of *H. ater* occurred at both local and middle ranges of pine density (i.e., larger pine shelterbelts).

Another unexpected result of this study was that in the remote sites I captured more *H. ater* than *H. ligniperda*. Previous studies indicate that *H. ligniperda* is the more abundant species in New Zealand (Reay and Walsh 2001; Brockerhoff et al. 2006b; Mausel et al. 2007; McCarthy et al. 2010), but all of these studies took place in pine plantations or nearby. I propose four (not mutually exclusive) possible explanations for finding greater abundances of *H. ater* in remote locations: 1) *H. ater* may be able to colonize the root systems of damaged trees in pine shelterbelts, thereby using these resources as 'stepping stones' (Baum et al. 2004; Saura et al. 2014) to spread through and persist in the landscape; 2) *H. ater* has been in New Zealand ca. 35 years longer than *H. ligniperda* which might have allowed it to colonize more remote sites with low-density host material; 3) within pine plantations, *H. ater* could be an inferior competitor compared to *H. ligniperda*, which would be consistent with the greater abundance of the latter in areas with a high density of pines; 4) *H. ater* may be able to tolerate colder temperatures and wetter climates better than *H. ligniperda*. Initially, *Hylastes ater* was much more common in plantation forests after establishing but has since declined in areas where *H. ligniperda* is present (Reay 2000). However, in the southern half of the South Island where temperatures are cooler and where *H. ligniperda* has invaded more recently (post 2004) and populations are still very low, *H. ater* was still found at higher populations than *H. ligniperda* (Brockerhoff et al. 2006b).

Hylastes ater attacks the root systems of damaged trees in its native range (Eurasia) (Chararas 1962), and this has also been confirmed in New Zealand: I recently captured *H. ater* in emergence traps placed around the buttresses of damaged shelterbelt trees (Appendix B). It is important to note that this breeding in roots is different from the maturation feeding of *H. ater* on seedlings (Reay and Walsh 2002; Sopow et al. 2015). The ability of *H. ater* to reproduce and feed in different types of host material may explain why no strong association existed with pine plantations and why it was found in so many remote locations away from shelterbelts.

The likelihood of trapping *H. ater* or *H. ligniperda*, assuming they are present, is likely to be higher in areas distant from pine forests because of reduced competition between trap attractants (α-pinene and ethanol) and abundant host plant volatiles emitted by pine trees. This may explain the relatively high catch rates in remote locations compared to those in pine forests. Furthermore, as *H. ligniperda* appears to be more strongly attracted by α-pinene and ethanol lures than *H. ater* (Brockerhoff et al. 2006a), one would expect to trap more *H. ligniperda* than *H. ater* in remote locations if the two species were equally abundant.

Collectively, these circumstances indicate that *H. ater* is indeed more abundant in remote locations than *H. ligniperda*.

The limited information from other studies on long-distance dispersal by bark beetles, is generally consistent with our findings. For example, Miller and Keen (1960) measured the dispersal of the western pine beetle *Dendroctonus brevicomis* from the natural pine forest edge to isolated patches of *Pinus ponderosa* and concluded that beetles dispersed between 3.2 km and 30 km. *Dendroctonus valens*, invasive in China, was recorded dispersing 20 to 35 km in the Luliang and Taihang mountains (Zhang et al. 2002). In the United States, Smith (1970) reported *D. valens* flying distances of up to 16 km. Flight mill studies conducted in laboratory settings have provided estimated flight distances of *Dendroctonus* and *Ips* bark beetles of up to 45 km (Atkins 1961; Jactel and Gaillard 1991; Byers 2000). Long-distance dispersal events aided by wind must also be considered an important mechanism for spread that could potentially displace bark beetles over great distances (Nathan et al. 2003). One study showed that airborne mountain pine beetles (*D. ponderosae*) were found at 800 m above the forest canopy and with wind assistance could spread 30-110 $km \cdot day^{-1}$ (Jackson et al. 2008). While it is clear that bark beetles are capable of long distance dispersal, it is less clear what cues signal beetles to land and what the fates are of beetles that land in remote locations without any host resources. Currently, two main mechanisms are proposed for how bark beetles find suitable hosts at close range: primary attraction and random landing (Saint-Germain et al. 2007). The primary attraction hypothesis states bark beetles utilize host volatiles to locate host resources and directly fly to the correct host (Person 1931). There is clear evidence that most conifer-infesting bark beetles have the ability to distinguish host from non-host volatiles (Zhang and Schlyter 2004); however, it has also been shown that non-host volatiles can interfere with the ability of a pine bark beetle (*Ips sexdentatus*) to orientate towards conspecific pheromones or host volatiles (Jactel et al. 2001).

Saint-Germain et al. (2007) define the random landing hypotheses, "insects fly and land on trees at random and then assess their quality as potential hosts using short-range olfactory and gustatory cues". These authors found that random landing was common in Cerambycidae, but less so in Scolytinae, in combination with primary attraction (Saint-Germain et al. 2007). That is, habitat patches were recognized by primary attraction but individual trees within a patch were reportedly found via random landing; however, this study took place at a rather small scale (2 – 10 m). In our study, which took place on a much larger scale, I propose that random dispersal of *H. ater* and *H. ligniperda* occurred at a landscape scale (i.e., to a forest or remote valley) and primary attraction was used to locate host cues in our traps. It is unlikely that *H. ater* and *H. ligniperda* were able to distinguish small amounts of primary attractants while undergoing long distance dispersal across forested mountain regions of the Southern Alps. Finding a suitable host post-landing is a multistep process dependent on the physiological state of the beetle and local environmental conditions (Wallin and Raffa 2000).

As an alternative to long distance dispersal, the movement of firewood and timber could explain the occurrence of *H. ater* and *H. ligniperda* in areas without host resources; it is a known pathway for the

movement of other bark beetles (Haack et al. 2010b). On Stewart Island for example, pine firewood is commonly moved across Foveaux Straight from the South Island, and I suspect this is the most likely pathway for the invasion of *H. ater* onto the island.

In scenarios where bark beetles randomly disperse and invade previously un-colonized suitable host-patches, establishment becomes dependent on host density, landscape structure and propagule pressure (Lockwood et al. 2005, Nowicki et al. 2014). Additionally, as insects disperse across a landscape, the chances of population establishment decrease with increasing distance from source populations; Allee and stochastic effects may limit the capacity for low-density populations to establish (Tobin et al. 2007), leading to a "range-pinning" effect (i.e., population establishment thresholds create an abrupt edge at the limit of a species' spatial distribution) (Keitt et al. 2001). However, it has recently been proposed that spread can still occur through a landscape if a portion of habitat patches have reduced Allee thresholds (Walter et al. 2016).

In the present study, I found that two highly successful non-native saprophytic bark beetles were remarkably effective dispersers and their main limitation for range expansion appears to be the shortage of host material in a heavily fragmented landscape away from larger continuous pine forests. That such small beetles appear to have very high dispersal capabilities is important for understanding the processes determining which species are successful biological invaders. These mechanistic insights into the spread and persistence of *H. ater* and *H. ligniperda* in a fragmented landscape provides ecologists, government agencies and land managers with a better understanding of factors leading to successful invasion events, even across a fragmented landscape.

Chapter 3 – Allee dynamics at the limit of *Ips pini* range in a fragmented landscape

Introduction

A species distribution is not fixed in space or time. Indeed, species range limits dynamically expand and contract with fluctuations of resource availability, interspecies competition, disturbance events and abiotic determinants (Sexton et al. 2009; Godsoe et al. 2015). Dispersal is a critical mechanism driving species to expand their range limits, sometimes beyond regions fulfilling niche requirements, forming sink (non-self-sustaining) populations that may eventually go extinct (Holt 1985; Pulliam 1988; Dias 1996; Kubisch et al. 2014). Sink populations can persist through the rescue effect where immigration exceeds emigration (Gotelli 1991), but local source populations may also face extinction if too many individuals leave (Holt et al. 2005). Clearly, the study of species range limits and distributions is complex.

Habitat fragmentation, induced by humans or natural disturbances, can affect levels of emigrations relative to population growth, sometimes leading to a loss of species (Andow 1990; Hanski, 1991; Fischer and Lindenmayer 2007; Ronnenberg et al. 2013; Haddad et al. 2015). Negative consequences of fragmentation have been observed in mammals (Bright 1993), birds (Amos et al. 2014), insects (Hanski et al. 1996; Tscharntke et al. 2002), frogs (Gibbs 1998) and woody plants (Vranckx et al. 2011). In some cases, habitat fragmentation can actually benefit populations, such as avian nest predators (Chalfoun et al. 2002), mistletoe pollination (Burgess et al. 2006), and coral-associated reef fishes (Bonin et al. 2011). Reconnecting habitats and understanding the barriers that impede dispersal is a major focus of conservation ecologists hoping to prevent species extinctions (Haddad et al. 2015; Vasudev et al. 2015). Empirical, theoretical and conservation ecologists are charged to work collaboratively to reduce the global impacts of habitat fragmentation on species biodiversity (Hanski 2015).

The addition of habitat patches to a landscape can also facilitate the spread of non-dispersal limited species into novel environments (Harrison and Bruna 1999). In New Zealand, for example, no native species of *Pinus* (pines) were present until humans planted them for production purposes (continuous pine plantations) and agricultural windbreaks (discrete isolated patches). Now, a suite of non-native pine-feeding invertebrates are established and have spread through most of the country (See Chapter 2, Brockerhoff et al. 2006b). One hypothesis explaining how some non-native invertebrates spread between the larger continuous patches is the utilization of isolated discrete patches as "stepping stones" which provide temporary residence for individuals moving through the landscape (Chapter 2). Saura et al. (2014) recently declared the importance of habitat stepping stones, stating that sufficiently

large patches can serve as a transition pathway for species dispersing between larger continuous habitats (see also Baum et al. 2004).

Both habitat and population density thresholds must be met for a species to persist in discrete habitats. Populations are predicted to persist in discrete habitats if the metapopulation capacity (i.e. the spatial structure, habitat quality and volume of habitat) is above a threshold value determined by the properties a species needs for positive growth (Hill and Caswell 1999; Hanski and Ovaskainen 2000; Thomas et al. 2001). Additionally, bistable Allee effects can determine population persistence in discrete habitats when densities fall below a critical threshold; this pattern is not observed in non-fragmented habitats, where species persistence occurs even when rare due to local demographic rescue (Keitt et al. 2001; Holt 2009). Population extinctions can also occur because of demographic and environmental stochastic processes, especially in conjunction with Allee effects (Lande 1998; Liebhold and Bascompte 2003). Invasion pinning (or propagation failure) occurs when dispersing populations fail to establish in discrete habitats because of strong Allee effects (Allee 1938; Keitt et al. 2001; Taylor and Hastings 2005; Kanarek et al. 2013). Allee effects are sometimes variable in space and time and can vary spatially with landscape structure (Walter et al. 2016).

In the Midwestern United States, a fragmented mosaic of planted pine windbreaks (or shelterbelts), small pine plantations and plantings of individual trees for ornamental purposes have been introduced to the landscape, an area historically free of pines (Macdonald et al. 1998) and heavily subjected to intense agriculture (Swihart et al. 2003). These plantings provide a unique opportunity to study how the addition of habitat fragments to a landscape adjacent to continuous forests may promote the expansion of herbivore species range limits. In this study, I used a single species model organism, the native pine engraver beetle *Ips pini* Say (Coleoptera: Scolytinae), to determine what levels of pine density and distance from large source populations are associated with declines in trap capture rates, thereby informing where in the fragmented landscape local populations of *I. pini* may reproduce or be pinned.

Methods and materials

Study system: Ips pini

Ips pini Say (Coleoptera: Scolytinae) is native to most of North America, wherever its hosts (*Pinus*) are found though it is absent from the south eastern USA (Lanier 1972). As a secondary bark beetle, *I. pini* prefers physiologically stressed *Pinus* trees (Schenk and Benjamin 1969). Therefore, a single pine tree or a patch of pine trees does not always provide suitable host material. Dispersing *I. pini* males first colonize *Pinus* hosts and release ipsdienol which attract both male and females (Schenk and Benjamin 1969). Aggregations of larger numbers of *I. pini* in a single tree increase the probability of successful colonization but also may result in shorter egg galleries and reduced reproductive success

(Robins and Reid 1997, Chapter 4). Reproduction of beetles in logging operation slash can lead to elevated densities, allowing colonization of relatively healthy trees in Idaho (Livingston 1979). *Ips pini* is also considered an important pest of red pine (*Pinus resinosa*) plantations in the Great Lakes Region (Klepzig et al. 1991, Erbilgin and Raffa 2002). In Canada, *I. pini* has been listed as a major pest (Safranyik 1995).

Study area and experimental design

I placed a network of insect funnel traps from the edge of the eastern pine forests (82° W longitude) in Ohio to eastern Iowa (92° W) (Fig. 3.1). I utilized historical trapping records of *I. pini* (Atkinson 2013) to determine the extent of the experimental transect, with the objective of extending the transect west until *I. pini* populations decline to near zero. The network consisted of installing three pairs of Lindgren multiple-funnel traps across 8 north – south transects (Fig. 3.1). Pairs of traps were separated by ~20 km and traps within a pair were separated by > 2 km. I placed 1 north – south transect (transect 1) within the eastern pine forests to compare trap capture with western traps during the same time period of exposure. Apart from the eastern most transect placed in the eastern pine forest, all other transects were placed in a rural landscape dominated by corn and soybean. Individual pine trees, small pine shelterbelts and very small pine plantations (< 1000 trees) were present but very uncommon throughout the Midwest.

Synthetic lures containing the sex pheromone of *I. pini*, ipsdienol (release rate determined by manufacturer: 0.1 – 0.3 mg/d at 22-25° C) (Synergy Semiochemicals Corp., Burnaby, BC, Canada), were paired with 12–funnel insect traps.

The total trap deployment time in both 2014 and 2015 was 14 weeks. In 2014, traps were deployed 30 May – 26 August, however, it was determined that this failed to overlap with the early portion of *I. pini* seasonal flight period, so in 2015 traps were deployed earlier, from 13 April -24 July. Traps were checked approximately fortnightly for *I. pini*.

Measurements of pine density

Pine density in the vicinity of each trap was measured using two methods. First, a survey was made for all pine trees visible from roads within 2 km of each trap. The location, species, and physiological state (dead [no needles], dying [red needles] and alive [green needles]) was recorded for each tree (Table 3.1). Where large plantations or continuous pine forests existed, estimates of numbers of trees were made from satellite imagery (Google Earth Version 7.1.5.1557) and I assumed 3% of pines were dead and dying. This survey was conducted in July 2015, therefore, pines recorded as dying or dead were potentially in a different physiological state in 2014. Young pines (< ~3 m tall) were not recorded.

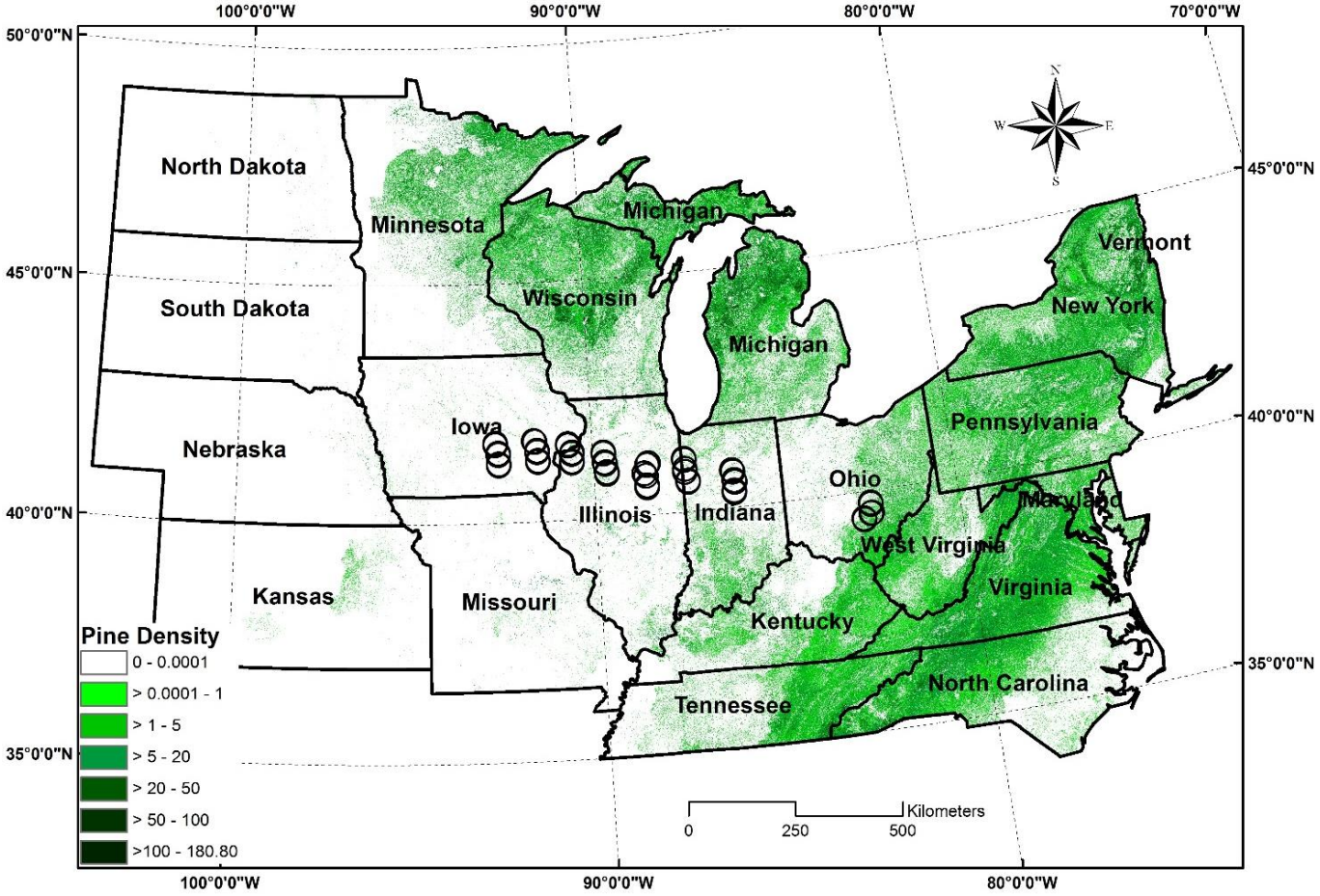

Figure 3.1 – *Ips pini* trap locations across 8 north - south transects (T) and pine density in Midwestern and north eastern United States. Black circles are placement of funnel traps in pairs (N = 48). Pine species used to create the map: *Pinus strobus*, *P. resinosa*, *P. nigra*, *P. virginiana* and *P. banksiana*. Pine density represents basal area within 5 km x 5 km pixels. The unit for pine density is ft^2/acre.

The second method for quantifying local pine density around each trap was to estimate a locally weighted average of a raster GIS layer quantifying pine basal area (ft^2/acre) interpolated from US Forest Service Forest Inventory and Analysis (USFS – FIA) plot data (Wilson et al. 2013). The average was calculated from all raster cells within 10 to 400 km of each trap weighted by the Gaussian dispersal kernel:

Equation 3.1

$$g = exp\frac{-|x_i - x_j|}{D}$$

where $x_i - x_j$ is Euclidean distance (between each raster and the trap location) and D is the diffusion coefficient. The raster layer of pine basal area quantified density of all pine species.

I tested five values of$D$: 0.1, 2, 5, 10 and 50. The lowest values of D weight local pine densities more heavily than the largest values of D (Fig. 3.2). I also calculated distance weighted averages of pine density within distances of 10, 200 and 400 km from each trap (N = 48) to account for local, intermediate and distant pine resources, respectively. I did not include pine species layers from Canada that would have been within the 400 km range. However, because the area of Canada (southern Ontario) that would have been included is mostly an urban and agricultural area that contains little pine, this likely had little effect on results.

It is important to note that *I. pini*, usually only utilizes stressed and declining trees as hosts (Schenk and Benjamin 1969, Kopper et al. 2004) so the presence of all pines does not directly indicate suitable habitat. However, for any cohort of pines, there usually is some fraction that comprise suitable breeding material and thus I assumed that the presence of pines in general corresponds to the presence of *I. pini* host resources.

Allee threshold estimation

Allee thresholds for *I. pini* were experimentally estimated by releasing fixed numbers of beetles and measuring colonization success in open and closed environments (Chapter 4). Field releases of beetles were conducted at sites near transect 8, where no naturally occurring *I. pini* were captured in 2014, see results. *Ips pini* releases were also conducted in an enclosed tent (closed environment) (Chapter 4). From these experiments, a component Allee threshold was estimated to range from 46 to 60 individual *I. pini*, based on the 50% probability of colonization success in the closed environment and the lowest number of beetles to colonize in the open environment, respectively (Chapter 4). Using this estimated Allee threshold, I investigated how pine density might limit the ability of *I. pini* populations to establish, based on trap capture data.

Table 3.1 - Mean and range of total, dead and dying pines per transect (N = 6 traps per transect) counted within 2 km of each trap (N = 48). I assumed pines in transect 1 (in the continuous eastern pine forest) and in plantations elsewhere contained 3% dead and dying pines.

	Transect 1		2		3		4		5		6		7		8	
Tree State	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Living pine	8619.3	407 - ~35, 556	777.3	369 - 2225	536.8	16 - 2346	270.2	56 - 607	237	11 - 1028	895.7	171 - 2254	181.5	37 - 380	752.5	54 - 2200
Dead pine	21.8	12 - 1067	14.5	2 - 60	26.2	0 - 148	2.8	0 - 15	6.5	0 - 37	14.7	0 - 45	2.8	0 - 7	19.5	0 - 60
Dying pine	0.2	12 - 1067	11.2	1 - 60	20.7	0 - 123	1	0 - 5	4.8	0 - 27	12.7	0 - 45	0	0	19	0 - 60

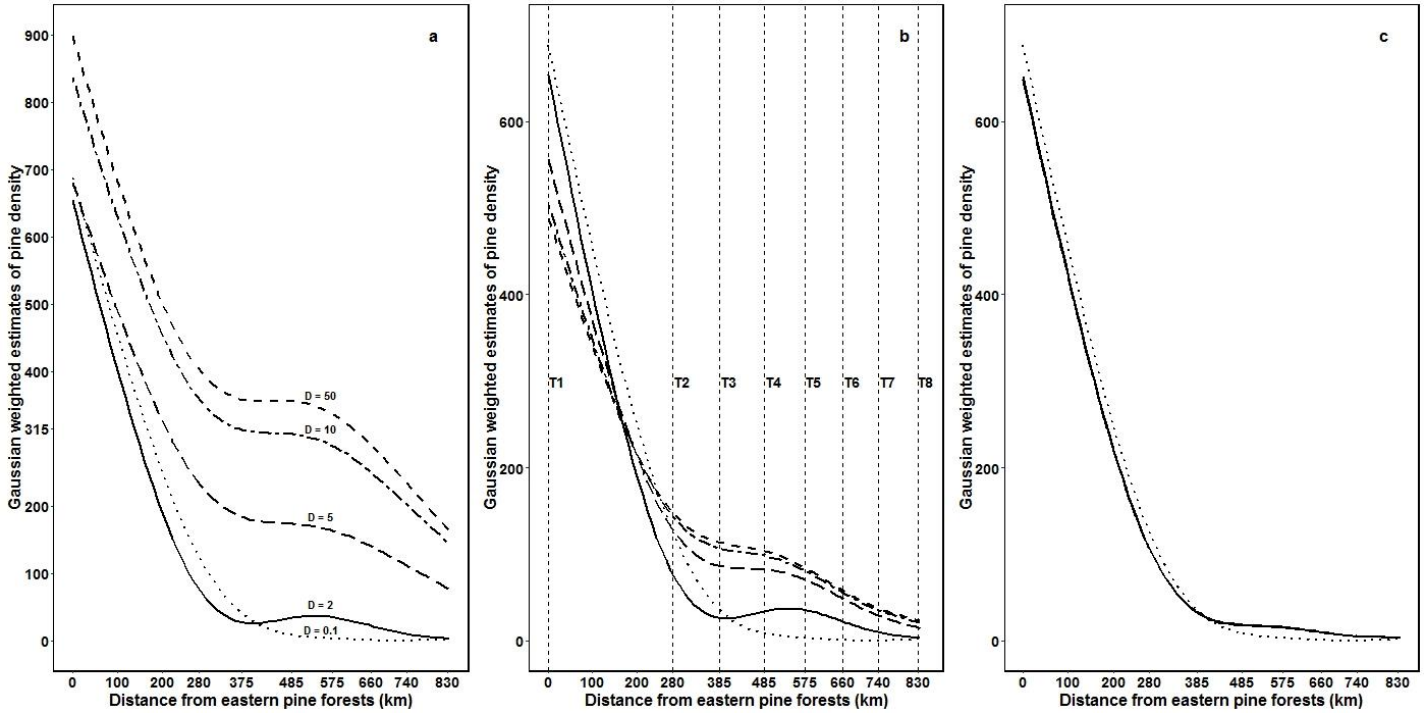

Figure 3.2 – Estimates of pine density from a Gaussian kernel function (equation 1) in relation to distance from the edge of the eastern pine forests (Ohio) to Iowa. Estimates were calculated within 400 (a), 200 (b) and 10 (c) km of each trap (N = 48). In (a), each line was created with the above D (the diffusion coefficient) and lines in (b) and (c) were created with and correspond to the same values. A value of D = 10 indicates pines near and far away are more equally weighted (e.g. the red pine forests of Minnesota and Wisconsin are equally weighted with local pines for foci [traps] in Iowa). A value of D = 0.1 indicates only local pines are accounted for because the distance decay function decreases pine values rapidly away from the foci. Lines were created with a GAM smoother (trap distance ~ Gaussian estimate, knots = 5). Vertical lines in figure 2b represent locations of 8 north - south transects (T) along the east – west transect.

To make this comparison, I converted trap capture data into the numbers of *I. pini* I would expect to catch in an ipsdienol trap if I had released them, as in the Allee threshold determination experiments. This conversion was based on the recapture rate (9.5% for traps placed 5 m away) from a previous *Ips typographus* release-recapture experiment conducted by Duelli et al. (1997); unfortunately, no release-recapture experiments have been conducted for *I. pini*. I chose to use this recapture rate because it is the only study I found that measured a recapture rate within similar distances as our release experiments (1 and 10 m). This assumption can be at least partially justified based upon the taxonomic and behavioural similarity previously observed between these species. Biweekly counts were converted to *I. pini* catch per trap per day to account for the majority of released insects typically being captured in the first day of release recapture experiments (Jactel 1991; Franklin et al. 2000). I then paired *I. pini* catch per trap per day with the recapture conversion factor to obtain an estimate of the expected pseudo-release density, assuming that 10% of released beetles are attracted to the ipsdienol trap. This estimate allows us to make predictions of *I. pini* colonization success based on an Allee threshold at different pine densities based on trap location. I highlight that the empirically derived Allee threshold and the pseudo-release density of *I. pini* are approximations that will fluctuate with changes in abiotic and biotic pressures through time and space.

Statistical analysis

All statistical modelling was conducted in the R language (V. 3.2.3, R Development Core Team 2015). The total number of *I. pini* captured in each trap over the entire year was modelled as a function of spatially weighted averages and road survey counts of pines using negative binomial regression with a log link (MASS package, Venables and Ripley 2002). The negative binomial distribution allows for overdispersion of count data, eliminates the possibility of negative values and allows Akaike's information criterion (AIC, Akaike 1973) to be calculated for model comparison (Hilbe 2007; Zuur et al. 2009). This model expresses the likelihood of trap capture of *I. pini* in relation to pine density for each trapping season. Spatially weighted estimates of pine density calculated using different scaling factors D were collinear (detected by a variance inflation factor test [car package R, Fox and Weisburg 2011]) because of the nested spatial structure of the data, therefore, I ran individual tests for each value of D. I also included two binary predictors in the model for trap location (in pine trees or not, and "open space" i.e. not surrounded by forest, such as a trap hung in a tree at the edge of a corn field, or not). A backward elimination procedure, using a χ^2 likelihood ratio test (LRT) with the drop1 function (R), set at $\alpha = 0.05$, along with data visualization techniques (Zuur et al. 2010) and AIC, were used to determine final models for each year. The explained deviance (pseudo R^2) was calculated for each model following Dobson (2002). Outliers were determined by a Cook's distance > 1.

To better understand where local *I. pini* populations (inferred from trap capture data) fall below the estimated Allee threshold in relation to spatially averaged values of pine density, I used a three-

parameter nonlinear least squares model (nlme package, Pinheiro et al. 2015). I ran separate models for *I. pini* trap capture during spring emergence and post spring emergence, using the 400 km pine density at D =10. By graphically incorporating the estimated Allee threshold (see above), inferences can be made as to where *I. pini* populations are likely to go extinct, persist or be stably established.

Results

Ips pini trapping results

As expected, decreasing numbers of *I. pini* were caught per trap with increasing distance from the eastern pine forests (i.e. trap capture decreased moving east to west) in both 2014 and 2015 (Fig. 3.3). In 2014, a total of 5,005 *I. pini* were captured between 30 May – 26 August, of which 55% were female and 45% were male (Fig. 3.4a). I captured 62% of all *I. pini* in 2014 within the eastern pine forests (transect 1); the single highest trap catch for the season (N = 1,231, 25% of total 2014 catch) also occurred in transect 1. Zero beetles were captured in the six traps in the western most transect (transect 8).

A similar pattern of decreased *I. pini* trap capture with increasing distance occurred in 2015 (Fig. 3.3). However, because I started trapping earlier to capture the initial wave of spring emergence beetles, differences did exist between 2014 and 2015. I captured a total of 27, 412 *I. pini* but 22,123 (81%) were captured in the first trap check following the beetles' spring emergence (13 – 27 April). Transect 2 contained the highest individual single-trap catch during the spring emergence (N = 12,383, 45% of total 2015 catch) and post spring emergence (N = 906, 3% of total 2015 catch) (Fig. 3.3). In the western most transect (transect 8), I captured 7 *I. pini* in 2015 during spring emergence and 1 *I. pini* post spring. The sex ratio of all *I. pini* captured, including spring emergence, was 51% female and 49% male (Fig. 3.4b).

Effects of spatially averaged pine density on Ips pini trap capture

At 200 km and 10 km (Fig. 3.2 b and c), estimates of pine density remained very low for all D in the western most transects (T3 – T8), reflecting the low number of pine patches in this area. However, when long distances were considered (400 km, Fig. 3.2 a), estimates of pine density increase with increasing D in the western transects because red pine (*Pinus resinosa*) forests in Wisconsin and Minnesota (Fig. 3.1) are accounted for. Also, spatially weighted estimates are not strongly affected by the presence of small quantities of pine but were mostly driven by the presence of larger patches of pine forest. Therefore, in the final negative binomial models, I only used spatially weighted averages of pine density obtained from 400 km to account for the possibility of long distance dispersal and local pine density obtained from the 2 km physical surveys to account for local dispersal.

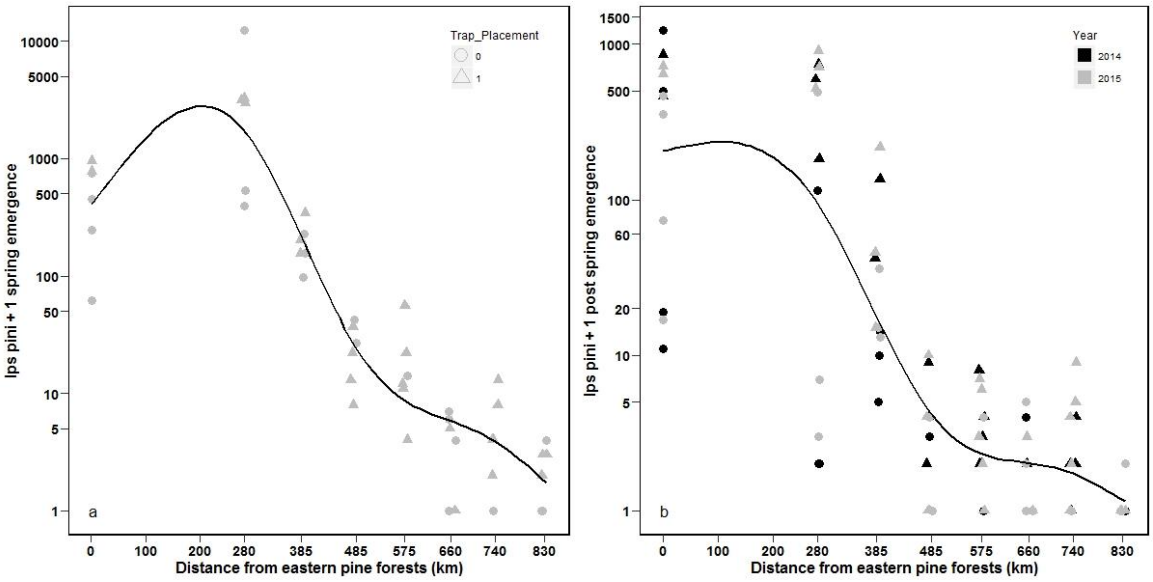

Figure 3.3 – Trends of *Ips pini* trap capture with distance from the eastern pine forests (distance = 0 km) to south eastern Iowa in 2014 (black symbols) and 2015 (grey symbols). Circles represent traps placed in enclosed areas and triangles are traps placed in open space. (a) - spring emergence of *I. pini* in 2015 (13 – 27 April). (b) – combined 2014 (30 May – 26 August) and 2015 (27 April – 24 July) post spring emergence. The smoother line is a GAM fit (*I. pini* ~ trap distance, knots = 5) intended to show the general pattern of the data. *Ips pini* data was scaled with a log10 transformation. Note y – axes were log scaled and y – axis values are different.

Regression models indicated that the abundance of both nearby and distant pine resources were important in predicting *I. pini* trap capture in 2014 and 2015 (Table 3.2). A value of $D = 10$ gives relatively high weighting to distant pines (slow decrease in weighting with increased distance) (Fig. 2), which implies that long distance dispersal by *I. pini* influences local trap catches.

In 2014, *Ips pini* trap captures were greater when traps were hung in trees not surrounded by forest (Table 3.2). In 2015, both during and post spring emergence *I. pini* trap captures increased when traps were placed in pine trees (Table 3.2).

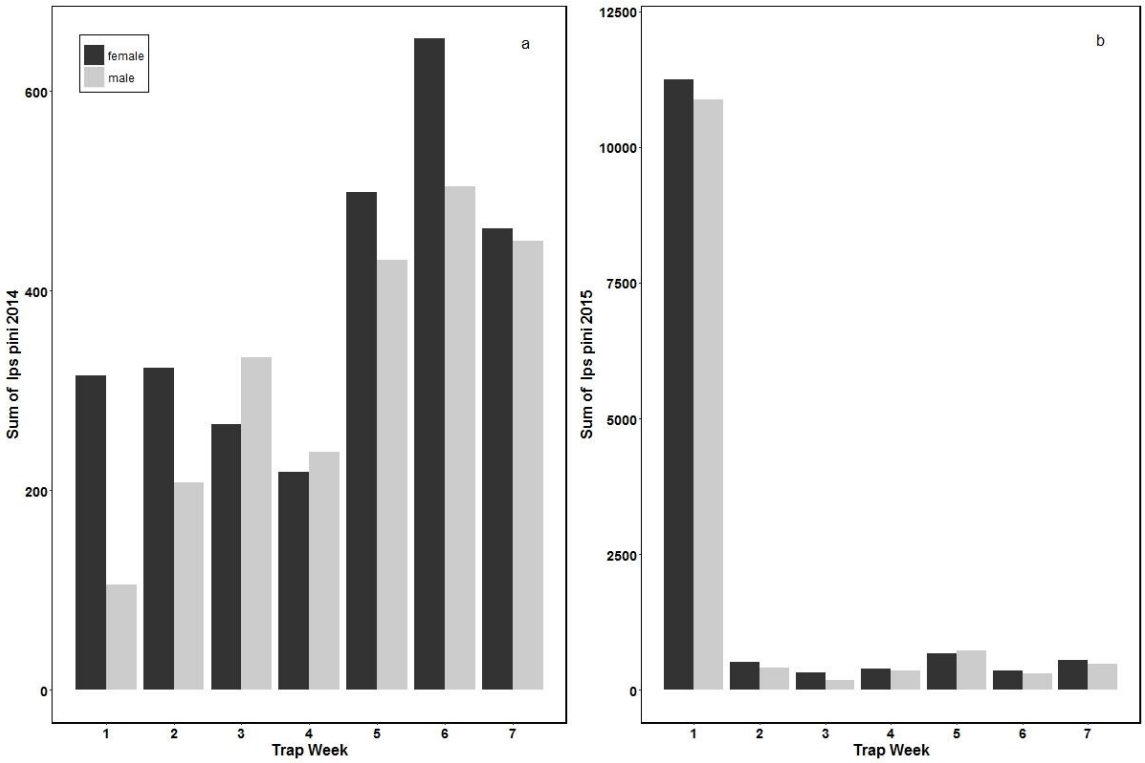

Figure 3.4 – Numbers and sex ratio of *Ips pini* captured across the 7 week trapping periods in 2014 (a, 30 May – 26 August) and 2015 (b, 13 April – 24 July). Note that y-axis values are different.

Allee effect application

Figure 3.5 displays *I. pini* trap capture rates against regional abundance of pines (400 km weighted average of pine density). Best-fit models were used to predict where *I. pini* local populations during and post spring emergence would be predicted to establish, persist or go extinct day to day based on an empirically derived Allee threshold (horizontal lines on Fig. 3.5).

During spring emergence (Fig. 3.5a), a large pulse of *I. pini* pushed local abundance above the estimated Allee threshold in transects 1-3. Daily trap capture in transects 4 and 5 were either close to or below the Allee threshold indicating establishment may fail. However, if *I. pini* adults aggregate across multiple days and dying or weakened trees are available, local populations may establish. Trap capture of *I. pini* in transects 6-8 indicate populations will not establish because beetles never breach the estimated Allee threshold.

Post spring emergence (Fig. 3.5 b), continuing establishment of *I. pini* will likely occur in transects 1 and 2 but local populations in transect 3 fell below the Allee threshold. *Ips pini* trap capture in transects 4-8 indicate that establishment will not occur.

Discussion

With the addition of planted pines across a large landscape previously devoid of hosts, the distribution of *I. pini* has likely expanded. Both local and long distance dispersal from host resources are important in explaining *I. pini* observed distribution. Persistence of some local *I. pini* populations at intermediate values of host density appear to be dependent on a large pulse of spring emergence beetles that pushes local populations above the predicted Allee threshold. Even though I do not currently expect *I. pini* populations in western Illinois and Iowa, where local pine density is currently low and patches are highly isolated, to persist because of Allee effects (Keitt et al. 2001), beetles were still captured in these areas, indicating that dispersal is not the mechanism that prohibits range expansion. If humans continue to plant pines as ornamentals, windbreaks and plantations across the Midwestern landscape, thereby increasing host availability, I expect that the distribution of *I. pini* and other pine bark beetles will expand.

Ips pini distribution in regards to the Holt niche framework

Holt (2009) designated three ways that a species can persist within its population niche: 1. local population growth rate is pushed above its Allee threshold via large dispersal pulses 2. dispersers from multiple sources pooling (i.e. accumulating) 3. a change in the environment. I use this framework to discuss the observed distribution of *I. pini* in the Midwest.

1. Large dispersal Pulses

Persistence of *I. pini* populations at intermediate levels of host density appear to be dependent on large pulses of emergent beetles. Large pulses of *I. pini* during their flight season have previously been recorded. Gara et al. (1999) observed a spring pulse of *I. pini* in south-eastern Montana at the end of April 1992 and two subsequent (but smaller) pulses in mid-June and early-July corresponding to successive generations within the same year. Gaylord et al. (2006) detected spikes of *I. pini* in late summer and early autumn of 2002 and 2003 in central Arizona, as did Erbilgin and Raffa (2002) in west-central Wisconsin during 1998 and 1999. In Minnesota, Aukema et al. (2005) saw a pulse of *I. pini* in late August in 2001. Additionally, newly emerged *I. typographus* have been shown to fly greater distances than previously flown beetles, providing support that a migratory phase does exist for bark beetles (Duelli et al. 1997). In this study, I observed that a synchronized period of spring emergence resulted in a pulse of flying *I. pini*.

Table 3.2 - Deviance table for negative binomial regression of trap counts of *Ips pini* and associated predictors. Note that the model deviance and AIC is above the variables for each year.

Year	Variable	Estimate	DF	LRT	$P (> X^2)$	Model explained deviance
2014	intercept	-2.942				0.44
	living pine	0.004	1	8.27	**0.004**	
	dyingpine	-0.154	1	9.13	**0.002**	
	place	2.837	1	16.39	**< 0.001**	
	D = 10	0.010	1	14.96	**< 0.001**	
2015 - Spring Emergence Excluded	intercept	-1.354				0.43
	living pine *dyingpine	2.17×10^{-5}	1	10.33	**0.001**	
	hungingpinetree	2.229	1	20.69	**< 0.001**	
	D = 10	0.001	1	6.00	**0.014**	
2015 - Only Spring Emergence	intercept	0.189				0.25
	living pine	0.004	1	3.39	0.066	
	dyingpine	-0.158	1	4.35	**0.037**	
	hungingpinetree	1.343	1	3.61	0.057	
	D = 10	0.012	1	7.94	**0.005**	

trapdist = distance from individual trap to edge of eastern pine forest

deadpine = total number of dead pines counted during a physical survey within 2 km of each trap

living pine = total number of pines counted during a physical survey within 2 km of each trap

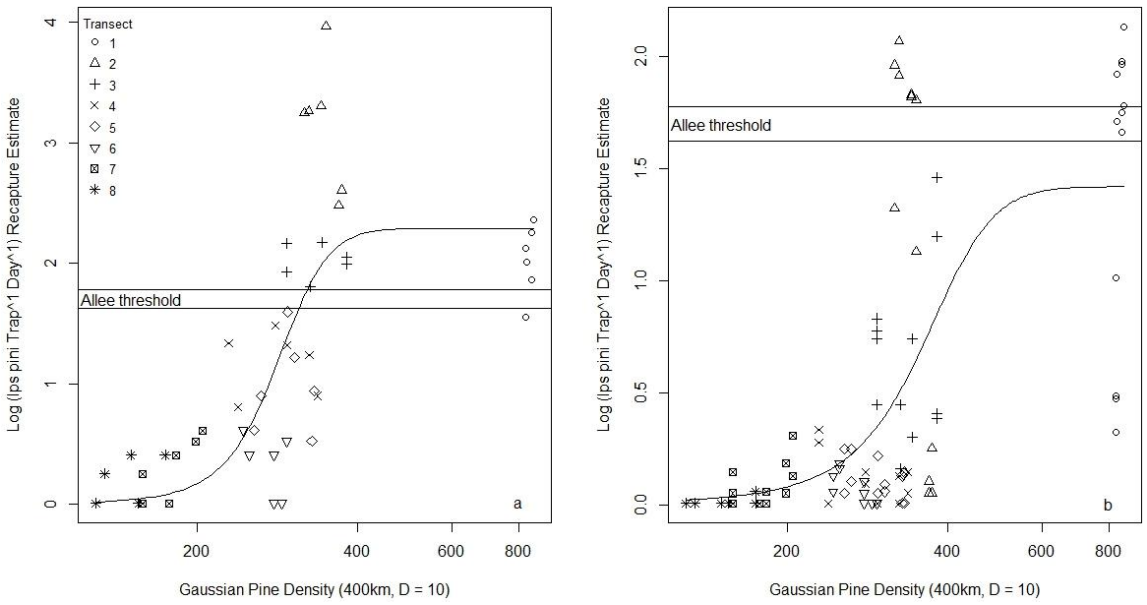

Figure 3.5 – Approximated *I. pini* per trap per day capture based on estimated pheromone trap effectiveness (10% of released *I. typographus* captured at 5 m, Duelli et al. 1997) in relation to Gaussian estimates of pine density within 400 km of each trap (*D* = the diffusion coefficient). (a) - spring emergence of *I. pini* in 2015 (13 – 27 April); (b) – combined 2014 (30 May – 26 August) and 2015 (27 April – 24 July) post spring emergence. The horizontal lines represent the estimated Allee threshold range for *I. pini* colonization. I predict populations above the Allee threshold are stably established, populations within or close to the Allee threshold can persist with a demographic rescue effect and populations distant from the Allee threshold will likely face extinction Data on the x-axis was scaled with a log10 transformation.

Dispersal of adults at these elevated levels into the fringe of their range limit may allow *I. pini* to overcome local Allee thresholds, potentially allowing populations to at least temporarily reproduce (Kanarek et al. 2015).

A theoretical study by Kanarek et al. (2013) showed that establishment of invading populations is more likely when organisms disperse less and aggregate at the invasion front in a continuous environment. Rhainds et al. (2016) provided support for this theory based on an observed mate-finding Allee effect of a longhorn beetle (*Tetropium fuscum)* at greater distances from a source population. Dispersal pulses of *I. pini* dispersing beyond their range limits are more likely to fail both because they may fail to locate hosts and the lack of conspecifics may limit their probability to locate mates and produce offspring (Chapter 4). Therefore, range expansion is more likely to occur when dispersing *I. pini* elevate local populations.

Synchronous dispersal pulses are not uncommon among bark beetles, especially those dependent on aggregation pheromones (Birch 1984; Wood 1982; Bentz et al. 2010). Synchronous aggregation is especially important for primary bark beetles (e.g., the mountain pine beetle

Dendroctonus ponderosae) that must overwhelm a tree's defence via mass attack (Aukema et al. 2008). *Ips pini* has been observed to synchronously emerge following or during emergence by the mountain pine beetle in British Columbia, a strategy that increases the availability of weakened pine trees (Raffa and Berryman 1980; Safranyik et al. 2004). Logan and Bentz (1999) have described synchronous emergence as adaptive seasonality because of the strong relationship between the development of bark beetles and seasonal temperatures. Successful establishment and persistence of some bark beetles is strongly correlated with adaptive seasonality (Logan and Powell 2001; Powell and Logan 2005).

2. Pooling of dispersers from multiple sources

The spatial arrangement and occupancy level of regional habitat determines the distributional range limits of organisms (Holt and Keitt 2000), especially in fragmented habitats (Hanski and Ovaskainen 2000, 2003). *Ips pini* populations in low density pine patches of the Midwest are likely supplemented by populations immigrating from continuous pine forests to the north, south and east (Fig. 1). Local populations of *I. pini* that are closer to adjacent pine forests to the north, south and east (transects 1 – 3) are more likely to receive immigrants and establish than populations distant from source populations in all directions (transects 6 – 8) (Sexton et al. 2009). Although highly unlikely, it is also possible that wind-aided dispersal could move individuals from western populations of *I. pini* in the Rocky Mountains to Midwestern states. A recent study found that *Dendroctonus ponderosae* disperses long distances (30 – 100 km per day) via aeolian dispersal above the forest canopy (Jackson et al. 2008).

Population establishment, or continuing persistence, is more likely to occur with a rescue effect (Gotelli 1991) of propagules moving through space from multiple source pools, especially at the edge of their range limit (Hanski 1991; Keitt et al. 2001). However, sink populations that are persisting via a demographic rescue (Hargreaves et al. 2014) may not always be supported because local source populations (also close to or just above the Allee threshold) are reduced because of emigration (Holt et al. 2005), thus reducing the number of source populations the following emergence.

3. A change in the environment

Lack of pine habitat is the main environmental limitation of *I. pini* establishment in the Midwest. Land use in the Midwest is dominated by agriculture and pines are not native to this region. Therefore, *I. pini* is currently dependent on human planting of pines for range expansion. However, even small plantations that are too isolated may not currently support *I. pini* persistence or establishment distant from source populations. For example, in transect 8 (around Oskaloosa, Iowa), 3 small pine plantations (all < 600 trees) were found with trees displaying signs of senescence within 2 km of the most southern trap, yet no *I. pini* were observed in either year. The future distribution of *I. pini* in the Midwest will depend on the spatial arrangement and density of planted pines.

Abiotic constraints are not a limiting factor for *I. pini* across the geographical space considered in this study. Both *I. pini* and their *Pinus* hosts have stable populations between latitudes 37° and 45°. Peak

emergences for *I. pini* have been observed when temperatures exceeded 17° C in Arizona (Gaylord et al. 2008) and reached 25° C in Idaho (Gara 1999), well within the reach of temperature ranges across this landscape. A key abiotic process that promotes population growth and establishment of several bark beetle species is disturbance events such as wind storms, flooding and fire (Veblen et al. 1994; Berg et al. 2006). High winds and flooding are not uncommon to the Midwest and can damage planted pines (e.g. tops broken by wind) or cause physiological stress (e.g. flooding induced root stress) to planted pines. Note also that bark beetles can behave as a disturbance agent and create positive feedback loops (Raffa et al. 2008), that, when acting with abiotic forces such as fire (Lynch et al. 2006), can lead to negative impacts on ecosystem services (Bebi et al. 2012). However, *I. pini* population eruptions are unlikely in this fragmented landscape because pine density is currently too low to support outbreak populations of bark beetles.

Application to invasive species

Keitt et al (2001) pointed out that "all species' ranges are the result of successful past invasions", therefore, parallels can be made between our observations in this *I. pini* system and non-native species establishment. Beyond *I. pini* range limit, dispersing propagules are invading new patches of habitat.

Likewise, non-native bark beetles, moved primarily by human transportation (Hulme 2009; Liebhold et al. 2012; Brockerhoff et al. 2014; Haack et al. 2014), are intercepted in small densities at ports of entry all over the world, yet colonization failure is more common than establishment (Williamson & Fitter 1996; Simberloff & Gibbons 2004). For example, over 103 bark beetle species (including *I. pini*) were intercepted in New Zealand between 1950 and 2000 but only a 11 (not including *I. pini*) have become established (Brockerhoff et al. 2006a). The likelihood of non-native bark beetle, and other non-native organism, establishment increases with the number of interceptions, representing propagule pressure (Lockwood et al. 2005; Simberloff 2009; Brockerhoff et al. 2014). Allee dynamics that may prevent population establishment of *I. pini* in the Midwestern fragmented landscape is also likely to prevent non-native species establishment in novel environments (Liebhold and Tobin 2008).

The mountain pine beetle has recently been considered an invasive pest in North America because of its northern and eastern range expansion into novel habitats of its ability to kill large swathes of pine forests (Aukema et al. 2008; Robertson et al. 2009) and the beetle's ability to colonize previously un-encountered host species (Huber et al. 2009; Cullingham et al. 2011; Cale et al. 2015). The mountain pine beetle has recently crossed geoclimatic barriers that previously prevented establishment, due in part to higher minimum winter temperatures (de la Giroday et al. 2012), providing a potential pathway to expand eastwards across the boreal forests (Nealis & Peter 2008; Safranyik et al. 2010). The mountain pine beetle exclusively attacks healthy trees and requires a critical mass aggregation of beetles to overwhelm the tree's defences, indicating that a strong Allee effect requiring higher densities of *D. ponderosae* exists. This is also the case for another mass aggregation bark beetle, *Ips typographus*,

whose establishment probability was found to depend on both a critical mass density of beetles and the distribution of fragments in the landscape (Kärvemo et al. 2016). It is known from interception frequency data that both *D. ponderosae* and *I. typographus* have been transported outside their native ranges on multiple occasions (Brockerhoff et al. 2003), yet neither beetle has established, possibly due to insufficient propagule pressure in the face of Allee effects.

In summary, I was able to quantify decreases in *I. pini* abundance associated with decreases in host abundance across a fragmented landscape by surveying across a large spatial scale. I found that a large synchronous emergence, may serve as a biological mechanism supporting *I. pini* persistence in intermediate host density ranges and expansion at the invasion front.

Chapter 4 – Component and demographic Allee effects in experimental bark beetle invasions

Introduction

Invasive species can have severe consequences on global biodiversity and economies (Clavero and Garcia-Berthou 2005; Simberloff et al. 2013). Fortunately, not all species arriving in novel environments become established (Keitt et al. 2001; Brockerhoff et al. 2014). A possible cause of establishment failure in invading populations is the demographic Allee effect (Taylor and Hastings 2005; Drake and Lodge 2006; Liebhold and Tobin 2008, Tobin et al. 2011), defined as positive density dependence at the population level (Allee 1931; Dennis 1989). Demographic Allee effects occur when a positive relationship exists between any component of individual fitness and population density (Courchamp et al. 1999), such as those associated with mate finding or predation saturation (Stephens et al. 1999). Although the role of Allee effects in population dynamics of invading populations is often considered, the majority of reports are theoretical (Boukal and Berec 2002; Courchamp et al. 2008), with relatively few empirical studies either in mesocosms (Kramer and Drake 2010; Gregory et al. 2010; Kaul et al. 2016a) or the field (Grevstad 1999; Kramer et al. 2009).

Certain biological traits are associated with higher probabilities of invasion success (for an overview see Kolar and Lodge 2001). Generalist species with *r*-selected life histories (e.g., rapid development, high fecundity or seed set, high population growth rates) tend to invade more readily (Sakai et al. 2001; van Kleunen et al. 2010). In addition, adult survival traits may be as important as reproductive potential for invading populations Sol et al. (2012). For any of these biological traits to be effective, however, the number of arriving propagules must exceed the Allee threshold, which varies based on their ability to find a suitable host (or habitat), successfully mate or be pollinated (in sexual organisms), and survive predatory, competitive and stochastic forces (Von Holle and Simberloff 2005). A greater understanding of this process will increase the understanding of biological invasion processes.

In this study, two species of bark beetles were used as models systems in the search for component and demographic Allee effects. Bark beetles are likely to show component and/or demographic Allee effects, arising not only because of mate finding failure but also arising as a consequence of the need to aggregate on hosts to overcome host defenses. Bark beetles in different feeding guilds were subjected to the same approach for quantifying a demographic Allee effect during the process of establishment. I first investigated a saprophytic bark beetle (*Hylurgus ligniperda* F.), which feeds and breeds in recently-dead woody material of *Pinus* spp. in contact with the ground. Female *H. ligniperda* can either mate with siblings in their development gallery or leave the gallery, colonize a new tree and mate. No sex pheromone is known to be associated with *H. ligniperda*. I also

investigated a secondary bark beetle (*Ips pini* Say), which utilizes living but senescing or damaged *Pinus* spp. Pioneer male *I. pini* initiate attack and emit a sex pheromone (ipsdienol) that attracts both males and females (Schenk and Benjamin 1969); males can mate with up to three females (Robins and Reid 1997). Because of the biological differences between these bark beetles (*I. pini* have to overcome tree resistance by aggregation in nature), I expect the strength of the Allee effect during invasion to be different for *I. pini* than for *H. ligniperda*.

To test the hypothesis that a critical population threshold must be overcome during the establishment phase of invasion, I empirically investigated establishment success for *H. ligniperda* and *I. pini* at different propagule pressures and spatial environments. These experiments were conducted to simulate an invasion event during the dispersal, host location and mate finding phases post beetle emergence. As per the definition of the Allee effect, I expected greater establishment success would occur at greater densities of released propagules. The information gathered here provides insight into the positive density dependent dynamics of invading bark beetle populations and details the biological traits that encourage or deter population establishment.

Methods and materials

Hylurgus ligniperda is native to Eurasia but has colonized many countries with pine plantations, including New Zealand where I conducted releases of this beetle. *Ips pini* is native to North America and has never colonized regions outside of its range, although it has been intercepted in New Zealand on 6 occasions (Brockerhoff et al. 2003). These species were chosen based on the ability to capture them in high numbers and release them in areas with little or no background populations of conspecifics (see Chapters 2 and 3).

I conducted releases of both *H. ligniperda* and *I. pini* in both field (open) and tent (closed) spatial environments (see sections below for specific details). By releasing beetles in both spatial environments at similar release numbers, I could approximate the effects of dispersal loss (field release) on colonization against a scenario where beetles could not escape. Dispersal loss has previously been cited as the cause of a component Allee effect for populations of the Glanville fritillary butterfly (Kuussaari et al. 1998).

For all release experiments with *H. ligniperda* and *I. pini*, I used trap-captured beetles. I did not use freshly emerged (or reared) beetles because it would have been logistically difficult to rear the numbers required, and because freshly emerged adults may not be physiologically ready to infest a host and mate. In contrast, I assume that previously flown beetles are in the process of actively searching for a host or a mate. Using trap captured bark and wood-boring beetles for release experiments is common practice (e.g., Zolubas and Byers 1995; Costa et al. 2013; Torres-Villa et al. 2013).

Hylurgus ligniperda releases

Live specimens of *H. ligniperda* were collected by capturing beetles in panel traps (baited with primary attractant lures, see Chapter 2 for details) placed in a recently harvested pine plantation in West Melton, Canterbury (43.28 S, 172. 23 E) in the Austral summer of 2014-2015. Adults were stored at ~12° C in an environmental chamber and beetles were held up to 2 weeks prior to use in experimental releases. Any dead or inactive *H. ligniperda* were discarded prior to releases.

Pinus radiata D. Don (Monterey pine) billets were harvested from plantation forests near West Melton, Canterbury, and Ikamatua, Westland (42.16 S, 171.34 E). Trees were cut into ~320 mm long billets and the cut ends of all billets were double-coated with paraffin wax to reduce moisture loss and desiccation. Billets were stored in a tent in order to exclude colonization by bark beetles and randomly chosen for field releases to reduce pseudo-replication. All billets were held < 1 month prior to use in experimental releases. All billets were also checked for infestation (e.g., presence of frass or boring holes) prior to releases.

Field releases of *H. ligniperda* were conducted in 6 areas, each area containing 4 sites, in the South Island, New Zealand (Table 1). Prior trapping in these areas confirmed the absence of *H. ligniperda* (Chapter 2). Release sites were separated by a distance > 1.5 km. For each release, I placed 4 *P. radiata* billets horizontally directly on the ground either 1 m or 10 m in 4 cardinal directions around a release platform (80 cm [long] x 8.8 cm [wide] x 2.4 cm [high]). I did not increase the number of billets with increasing distance because the goal of this study was to understand how colonization was affected by the distance to host resources and dispersal loss. All releases were conducted in grassy fields with no large objects (i.e., trees, shrubs, etc.) between billets and release platform. Releases were conducted on days with clear weather and temperatures were ≥ 18° C. The same methods were used to conduct releases in a closed environment (Biomesh™ tent, 2 m x 2 m x 2 m) where billets were placed 1 m from the platform. I used equal numbers of each sex for releases of ≤ 10 beetles; beetles were chosen at random for all other releases. All dead or immobile *H. ligniperda* were replaced with active beetles immediately before each release event.

Two types of controls were implemented to monitor for interference from background populations of *H. ligniperda* in field releases: 1) a control release of 0 beetles in 1 of the 4 sites was implemented at every release to monitor for external contamination from naturally established or released beetles from different sites; 2) panel traps were placed ~2 km from the most exterior release sites to monitor for locally flying *H. ligniperda*.

Billets were collected after 1 week of exposure in a tent or the field. Any *H. ligniperda* found on the exterior of the billet were individually separated and set aside for later re-introduction. Billets were transported to and stored in an enclosed dark room in 20 L polyethylene containers with mesh screens on the top and bottom to allow for airflow. *Hylurgus ligniperda* that were set aside were re-introduced to the same billet within the container. At 6-8 weeks following initial release, allowing suitable time for larval

development, billets were dissected with a wood chisel and searched for the presence of F1 larvae (abundance estimated in groups of 1's, 10's, 100's and 1000's). A portion of F1 living adults were separated to estimate sex ratio using the stridulatory chirp method (Mausel, 2002).

Ips pini releases

Live *I. pini* were captured in funnel traps paired with the secondary attractant ipsdienol (Synergy Semiochemicals Corp., Burnaby, BC, Canada) at various locations in south eastern Greene County, Pennsylvania, USA (39.75 N, 80.02 W) in 2015 (Table 1). Adult beetles were stored at ~14° C and no beetle older than 2 weeks were used for experimental releases. Only active *I. pini* were chosen for releases.

Pinus strobus L. (eastern white pine) billets were harvested from a small plantation near Mt. Morris, Pennsylvania (39.78 N, 80.15 W). Trees were cut into ~500 mm long billets and the cut ends of all billets were double coated with paraffin wax to reduce moisture loss. All billets were used for releases within 5 days of harvesting. Storage and infestation checking of billets was conducted in the same manner as for the experiment above.

Field releases of *I. pini* took place across 4 sites around Oskaloosa, Iowa (41.3 N, 92.65 W) (Table 1), an area that in 2014 was found to contain no resident *I. pini* (Chapter 3). Field release sites were separated by at least 2 km. Two fundamental differences occurred between releases of *I. pini* from *H. ligniperda*: 1) billets were all placed 10 m from the center release point in the open environment; 2) lures of the host primary attractants α-pinene and ethanol (30 mL of each compound) were placed on each billet (this was not done for *H. ligniperda* due to increased probability of interspecific interference). I placed lures on *P. strobus* billets because preliminary release trials in 2014 (at N = 25, 100, 250 and 500 *I. pini*; 6 billets in each trial at 10 m) without lures resulted in complete establishment failure. Primary attractants are present in all host material naturally colonized by *I. pini* so adding lures simply increases pre-existing levels of host attractants.

I used an even sex ratio at release densities of 10 or less. Releases were conducted on day with clear weather and high temperatures ≥ 18° C. All releases were conducted in uniform grass vegetation with no large barriers (trees, shrubs, etc.) between billets and release platform. Similar controls (local trapping and release control of 0 beetles) were also implemented for this experiment. Closed environment (screen tent, 3 m x 3m) releases were also conducted using *P. strobus* billets placed 1 m from a center release point (Table 1). No lures were paired with logs in the closed environment.

Pinus strobus billets were collected after 1 or 2 weeks of exposure in tents or in the field, respectively. No beetles were found on the exterior of billets in this experiment. After collection, billets were stored in enclosed cardboard tubes (either 0.15 m (diameter) x 0.61 m (length) or 0.3 m x 1.22 m).

Because *Ips* larvae cannot easily be identified to species and because a suite of pine infesting insects could have potentially infested the *Pinus strobus* billets, I waited at least 7 weeks between release date and dissection to allow for complete development of *I. pini* so I could count and identify adults. The same measurements and dissection methods of billets were used as in *H. ligniperda*. Numbers of male and female *I. pini* F1 adults were counted separately as sexes are easily distinguished using external morphological traits.

Table 5.1 – Numbers of bark beetles released for establishment success experiments in open (field) and closed (tent) environments

Beetle	Distance (m)	Environment	Release Size (# of times replicated)
Hylurgus ligniperda	1	closed	0(3), 5(2), 7(2), 10(2), 25(2), 50(2), 100(2), 250(2), 500(1)
	1	open	0(11), 10(6), 25(6), 50(6), 100(5), 250(5), 500(4)
	10	open	0(11), 10(6), 25(6), 50(5), 100(5), 250(5), 500(6)
Ips pini	1	closed	0(3), 2(2), 5(2), 7(2), 10(2), 15(2), 20(2), 25(2), 50(2), 75(1), 100(2), 500(2)
	10	open	0(5), 2(1), 5(1), 10(1), 25(1), 50(1), 60(1), 75(1), 100(1), 125(1), 150(1), 200(1), 300(1), 500(1), 600(1), 1000(1)

Statistical analysis

Data analysis was conducted in the R software language (V. 3.2.3, R Development Core Team 2015). To discern if *I. pini* and *H. ligniperda* were subjected to a component Allee effect during the colonization phase, maximum likelihood estimate analysis was conducted following techniques described by Kaul et al. (2016a, b). This analysis is robust because it produces estimates of a scale (λ) parameter, which informs what density of beetles are predicted for positive population growth, and a shape (k) parameter, which indicates the presence of an Allee effect when $k > 1$ (Kaul et al. 2016a). Replicate bark beetle releases were deemed as colonization successes (presence of F1 beetles) or failures (absence of F1 beetles), giving rise to a binomial distribution. A 2-parameter Weibull function was then fitted to establishment data, producing either a logistic or monotonic function. Where a logistic function was the better fit, the inflection point represents the critical threshold density required to overcome an Allee effect (Dennis 2002; Taylor and Hastings 2005).

I then used linear regression models to quantify the density dependent relationship between numbers of either F1 larvae (*H. ligniperda*) per adult released or F1 adults (*I. pini*) per adult released, and the number of beetles released in colonized billets. A positive density dependent response at this stage of bark beetle development indicates that a possible host conditioning component Allee effect exists. I also searched for a demographic Allee effect with linear regression by modelling F1 beetles per adult released against the number of beetles released for all replicates. Lower replacement rates at lower number of beetles released in these models indicate a demographic Allee effect exists.

Results

Hylurgus ligniperda releases

Only one occurrence of contamination in a field control billet was detected, where a single male *H. ligniperda* was found. In all billets deployed, no bark beetle species other than *H. ligniperda* were ever found.

In all release scenarios, *H. ligniperda* colonization was positively associated with the number of beetles released, indicative of a component Allee effect (i.e. $k>1$), (Table 2, Fig. 1a, d, g). However, the strength of the Allee effect varied with distance and spatial environment. In every scenario, at least one colonization event occurred even at the smallest number of beetles. The estimated critical threshold (inflection point) for *H. ligniperda* to overcome an Allee effect in the field was ~15 beetles at 1 m billet spacing (Fig. 1a) but was undetectable at 10 m (Fig. 1d); the critical threshold in the 1m tent release occurred at ~2 *H. ligniperda* and the shape of the function indicates that the Allee effect was very weak (Fig. 1g). The sex ratio of extracted *H. ligniperda* adults was 3.5:1 (300 females, 85 males) from 1 m field

billets and 9.25:1 (148 females, 16 males) from 1 m tent billets. It is assumed extracted adults were released beetles and not F1 adults.

Fig 1b,e,h quantifies the existence of a component Allee effect in the relationship between numbers of larvae completing development per adult released (only in billets that were colonized) in relationship to numbers released. A positive relationship between larvae per *H. ligniperda* released and adult released was only observed in the tent release ($F_{1, 36}$ = 86.01, P = <0.001, Adj. R^2 = 70%), indicative of a component Allee effect (Fig. 1h). The rate of larval production was not significant in 1 m field releases (Fig. 1b, $F_{1, 56}$ = 0.1, P = 0.8, Adj. R^2 = -2%). A negative density dependent in 10 m field releases occurred (Fig. 1e, $F_{1, 6}$ = 6.4, P = 0.04, Adj. R^2 = 44%), however, this relationship was based on a very small sample size (N = 6). of colonized billets.

Table 5.2 – Maximum likelihood estimates of bark beetle founder population Allee effects

species	scenario	λ (95% CI)	k (95% CI)	N_{min}
Hylurgus ligniperda	Field (1m, no lures)	3.11 (2.02 - 3.75)	3.12 (1.01 - 6.72)	10
	Field (10m, no lures)	14.47 (8.93 - 10)	1.33 (1.35 - 2.32)	10
	Tent (1m, no lures)	1.72 (0.02 - 3.01)	1.38 (0.05 - 5.29)	5
Ips pini	Field (10 m, with lures)	5.87 (4.83 - 10)	4.76 (0.78 - 11.38)	60
	Tent (1 m, no lures)	4.01 (2.51 - 10)	1.47 (0.1 - 3.44)	2

λ = the shape parameter where values > 0 imply beetle numbers needed for positive growth is larger than 1 mated bark beetle

k = the estimated shape parameter where a value greater than 1 indicates an Allee effect

N_{min} = the smallest release density to establish

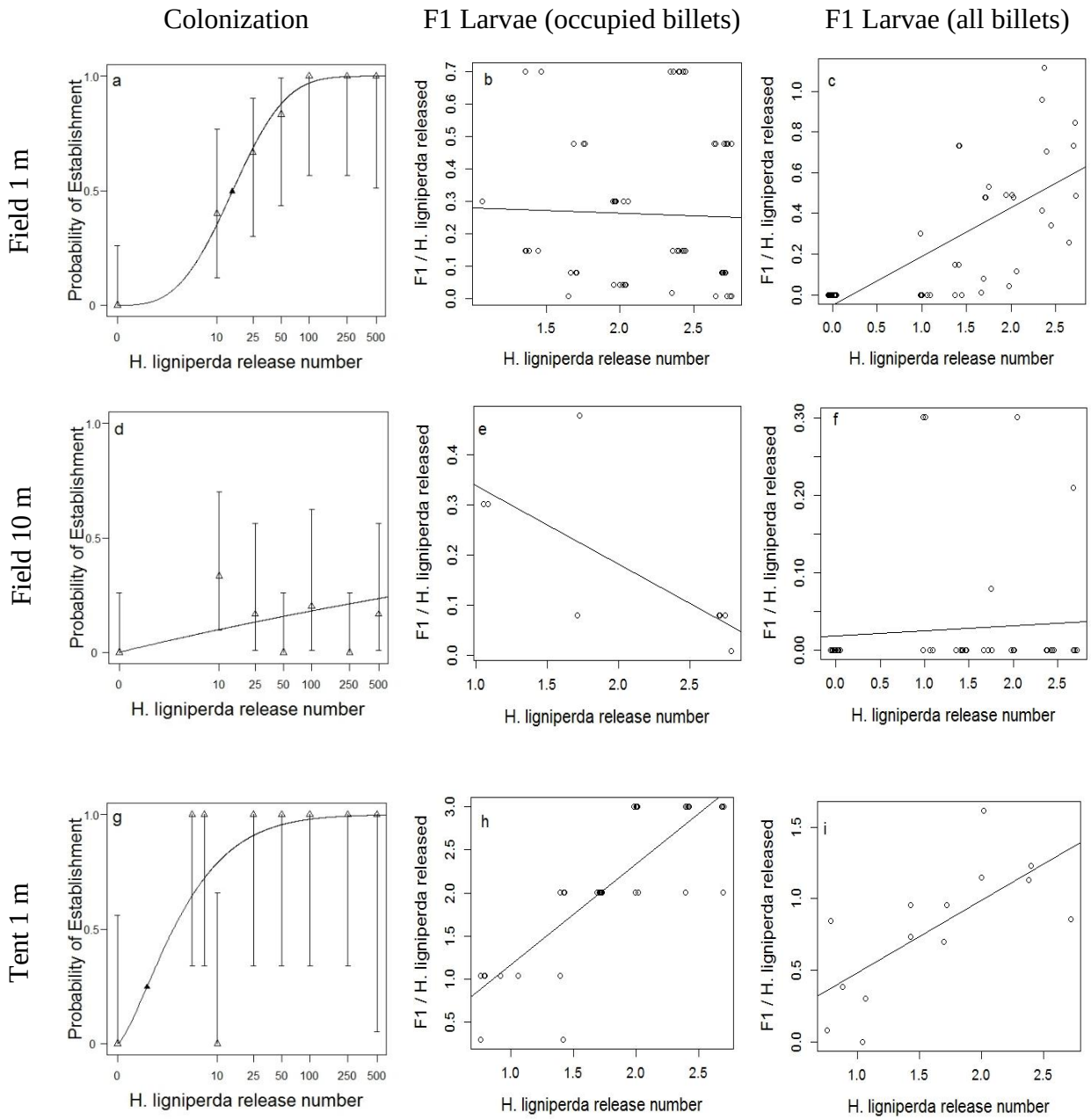

Figure 4.1 – Evidence for demographic and component Allee effects for *H. ligniperda* based on experimental field releases at 1m distance from billets (a, b, c), 10m distance (d, e, f), and in closed tents at 1m distance (g, h, i). Plots show the probability of colonization relative to numbers of beetles released (a, d, g), number of F1 larvae per adult released in relation to number of beetles released (b, e, h), and replacement rate in relation to number of beetles released (c, f, i). In b, e, h, c, f, i, lines were based on linear regression, but in a, d, g, the lines correspond to a 2-parameter Weibull function. The black triangle in a and g represents the inflection point indicating the critical threshold between the areas of the curve with positive and negative growth; the estimated critical threshold in d is beyond the plots x-axis.

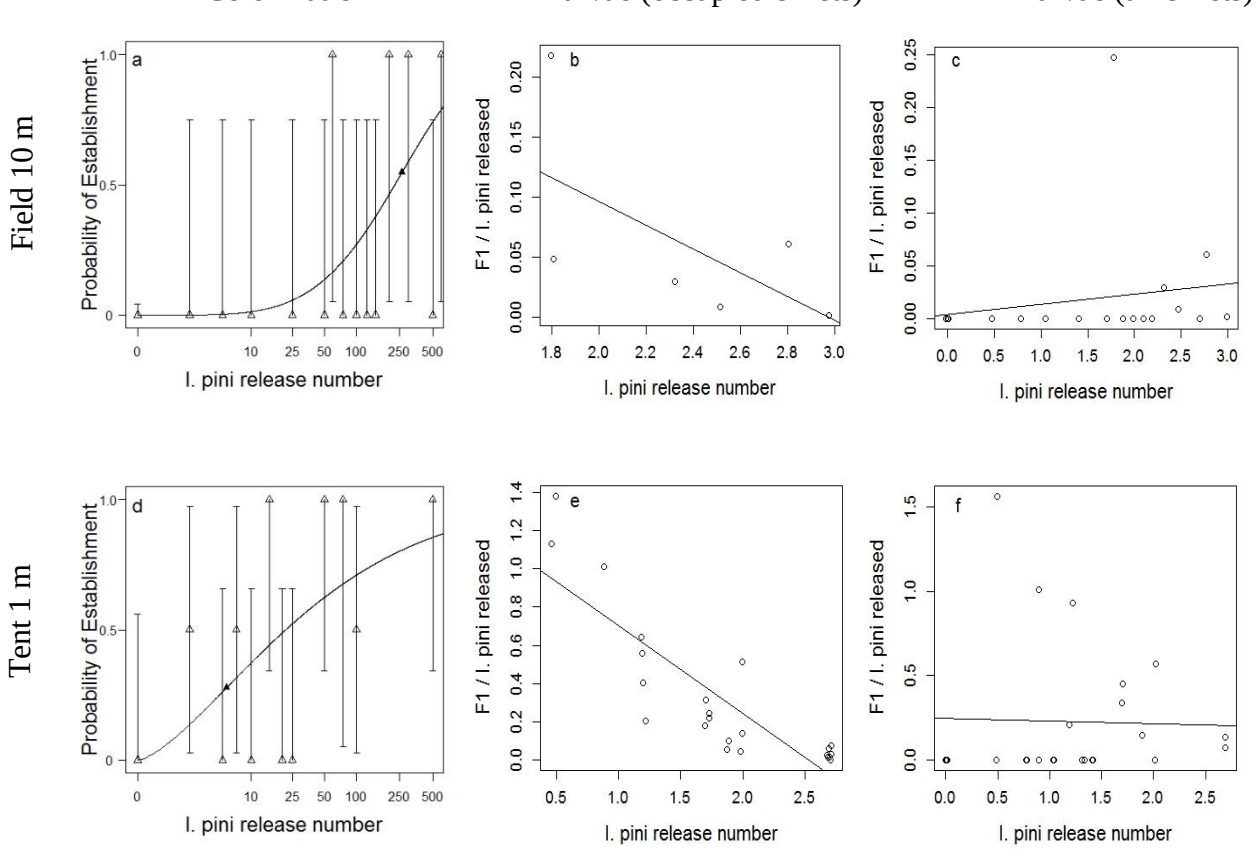

Figure 4.2 – Evidence for demographic and component Allee effects for *I. pini* based on experimental field releases at 10m distance from billets (a, b, c) and in closed tents at 1m (d, e, f). Plots show the probability of colonization relative to numbers of beetles released (a, d), number of F1 adults per adult released in relation to number of beetles released (b, e), and replacement rate in relation to number of beetles released (c, f). Lines and black triangles are same as in Figure 5.1

Ips pini releases

In field releases of *I. pini*, some billets were also colonized by *I. grandicollis* Eichoff. Six out of 15 (40%) release replicates (not including control releases of zero beetles) there was colonization by *I. grandicollis*. Of the six individual billets that *I. pini* successfully colonized, 2 were also colonized by *I. grandicollis*. However, it is unlikely that *I. grandicollis* had an effect on *I. pini* colonization, because *I. pini* were released immediately after billet placement.

Ips pini colonization was also positively associated with the number of beetles released and the strength of the Allee effect varied with distance and spatial environment (Table 2, Fig. 2a, d). The smallest beetle release size to colonize in field billets at 10 m was 60 *I. pini* and the predicted critical threshold occurred at ~265 beetles (Fig. 2a). In the tent scenario, colonization of *I. pini* occurred at the smallest release size (N = 2) and the predicted critical threshold occurred at ~7 beetles (Fig. 2d). Sex ratios of recaptured beetles in 10 m field billets and 1 m tent billets were 1.2:1 (88 females, 72 males) and 1.1:1 (524 females, 469 males), respectively.

A component Allee effect was also quantified for the relationship between *I. pini* F1 adults per adult released (only in billets that were colonized) and numbers of *I. pini* released (Fig. 2b,e). Unlike *H. ligniperda* which had a positive density dependent F1 response in tent releases, *I. pini* had a significant negative density dependent response (i.e., *I. pini* F1 production was highest at *lower* numbers of beetles released) in tent releases (Fig. 2e, $F_{1, 21} = 56.8$, P = <0.001, Adj. R^2 = 72%). In 10 m field releases (Fig. 2b), a significant relationship did not exist ($F_{1, 4} = 2.5$, P = 0.2, Adj. R^2 = 19%). Only 6 total billets were colonized by *I. pini* in field releases and larval production was low, reducing our ability to detect a component Allee effect. However, the negative density dependence observed in the tent releases was very strong (Fig. 2e), reflecting the relationship observed in the field (Fig. 2b). Although a component Allee effect was detected during colonization, a demographic Allee effect was not detected for *I. pini* tent (Fig. 2c, $F_{1, 22} = 0.02$, P = 0.9, Adj. R^2 = -0.04%) or field releases (Fig. 2f, $F_{1, 18} = 0.63$, P = 0.44, Adj. R^2 = -0.02%).

Discussion

Many theoretical studies have shown that component Allee effects can interact with each other (i.e. multiple component Allee effects, Berec et al. 2007) and with other density dependent processes (e.g., competition or predation) (Courchamp et al. 2000) in ways that may or may not produce a demographic Allee effect (Taylor and Hastings 2005). However, very few examples of experimental quantification of Allee effects exist. This is due, in part, to the difficulty of measuring low density populations. Here, I used an experimental approach using small populations in point introductions to probe for the existence of component and demographic Allee effects.

Bark beetles were a good model system to use because the potential for multiple component Allee effects arise not only from mate finding during colonization, but also from environmental conditioning and/or interactions with predators and symbionts (e.g. fungi, bacteria, etc.). Identification of component Allee effects (and their mechanisms) are important for determining how they may limit bark beetle (and other organismal) establishment and spread into new areas.

My results suggest that component Allee effects can occur in at least two stages – colonization and beetle development. During colonization, a component Allee effect was detected for both *H. ligniperda* and *I. pini*. Because lower numbers of released beetles are less likely to encounter each other, mate finding is a likely mechanism explaining this component Allee effect. *Hylurgus ligniperda* has no known secondary attractant, therefore mate finding may be more random than *I. pini*, where pioneer males attract both males and females with a sex pheromone. Sibling mating has never been confirmed for *H. ligniperda*, but may explain why I observed single galleries with 1 female adult and production of F1 larvae. In landscapes where *I. pini* is established, attracting conspecifics with secondary attractants is an effective strategy to locate mates, but during invasion where small numbers of beetles arrive at a single point in time and no resident population exists, this process may be disadvantageous.

Another mechanism which may reduce colonization success is dispersal loss. Kuussaari et al. (1998) found that dispersal loss in metapopulations of the Glanville fritillary butterfly was one mechanism (along with low mating success at low density) leading to an Allee effect. During experimental releases in my study, an immediate loss of individuals could occur from dispersal, reducing the numbers of beetles available to colonize the billets. This mechanism probably explains why critical Allee thresholds differed between field releases (Figs 1a, d and 2a), where individuals were not spatially bound, and tent releases (Figs 1g and 2d), where beetles were confined and not able to disperse. Dispersal loss itself is not a component Allee effect, but interacts with Allee effects and directly affects populations.

In the second stage of colonization (beetle development) that a component Allee effect was observed, density dependent responses were different for *H. ligniperda* (Fig. 1b, e, h) and *I. pini* (Fig. 2b, e). A potential mechanism explaining these responses is environmental conditioning by these bark beetles in association with symbiotic Ophiostomataceae fungi; both *H. ligniperda* and *I. pini* are associated with ophiostomatoid fungi (Klepzig et al. 1991; Jankowiak and Bilański 2013). The ability of beetles and fungus to colonize trees depends on the physiological state of the host (Klepzig and Wilkens 1997, Six and Wingfield 2011). As a saprophytic bark beetle, *H. ligniperda* prefers dead woody material (with severely reduced defensive compounds, drier host tissue and high oxygen content) whereas *I. pini*, a secondary bark beetle, prefers declining but living trees that still have a higher moisture content but also contain defensive compounds. In my experiment, where I used cut billets with waxed ends, moisture content would remain higher, defensive compounds would be highly reduced or non-existent, and desiccation would progress slower over time. Therefore, the reduced growth rate at fewer

released *H. ligniperda* in tents may have been related to better host conditioning by the beetle (and its associated fungi) at larger numbers. The counter-intuitive negative density dependent response of *I. pini* may be related to the fact that billet moisture content and chemistry ratio was favourable but trees were essentially defenceless, increasing the intraspecific competition within a very limited resource.

The observation that *I. pini* F1 production was negative density dependent is not unique. Robins and Reid (2007) found that reduced growth rates of F1 offspring occurred at higher aggregations of *I. pini*, and stated "… it remains perplexing why pine engravers [i.e., *I. pini*] aggregate actively in nature". Aukema and Raffa (2004) found that predator dilution is one benefit of aggregation; however, I propose three other alternative hypotheses: 1) locally, suitable senescing or damaged host trees may not be present. For population persistence to occur, *I. pini* may need to aggregate to overcome tree defences. This mechanism is risky because local populations would be investing all resources into a potentially adverse outcome if colonization was not successful, possibly resulting in local extinction; 2) colonizing *I. pini* may have relatively poor host detection capabilities compared to competing bark and wood boring beetles. Therefore, when a pioneer male is able to detect a host, it is more efficient for conspecifics to aggregate around the sex pheromone than search for a new host tree; 3) pioneer male *I. pini* have a reduced likelihood of recruiting conspecifics at greater distances from source populations because of limited propagules. To initiate a new population in a distant novel area, a strong aggregation pheromonal response would be beneficial. Higher F1 abundance at lower initial density could also provide a mechanism that allows population persistence to occur for smaller density long distance dispersing founder populations. Both my and the Robins and Reid (1997) studies were conducted in defenceless billets. It would be of great interest to conduct colonization experiments within living trees to determine if a positive density dependent response of *I. pini* would be found.

The combination of multiple interacting component Allee effects have been assumed to have a higher probability of leading to a demographic Allee effect (Courchamp et al. 2008). This assumption appears valid from our results, where two component Allee effects (Fig. 1g,h) led to a demographic Allee effect (Fig. 1i) for *H. ligniperda* in the tent release, but a negative density dependent response during *I. pini* development (Fig. 2 b, e) apparently offset a demographic Allee effect (Fig. 2c,f). As density dependent processes are extremely hard to identify, and their interactions with spatial scales make them even more complex (Berec et al. 2001), there could be other negative and positive density dependent mechanisms I have missed influencing the final demographic outcome.

Demographic and environmental stochastic, or random, processes must also be considered to have an impact on colonization and reproductive success (Lande 1998; Dennis 2002). Courchamp et al. (2000) found that small populations close to the critical Allee threshold may be at greater risk of extinction when stochastic processes are regarded. The differences I observed in critical Allee thresholds between tent and field releases (and distance between billets and release point) for both *H. ligniperda* and *I. pini* may partly be due to removal of negative stochastic strength in the tent environment.

The information acquired in this experiment can be broadly, but cautiously, applied to the expected Allee effects and invasion potential across the different bark beetle feeding guilds. The strategy of saprophytic beetles to attack recently dead host material makes them particularly likely to infest fresh cut timber in contact with the ground and thus exportation. As evidenced by the low Allee threshold estimated here for *H. ligniperda*, this group of bark beetles may be able to colonize novel areas at relatively low propagule pressures, thus, I rank this guild's invasion potential to be high. I rank secondary bark beetles' invasion potential to be intermediate based on the reduced probability of finding a host in a suitable physiological state and arriving in sufficient propagule density for individuals to find a mate. Seven out of 10 of the most commonly intercepted bark beetles in the USA that Haack (2001) reported were secondary bark beetles, but only one (*Hylurgops palliatus* Gyllenhal) has become established. *Hylurgops palliatus* is also the most commonly intercepted bark beetle in New Zealand (13% of all bark beetle interceptions) but is not yet established (Brockerhoff et al. 2006a). The most feared group of potential invasive species are the primary bark beetles (e.g., some *Dendroctonus* spp. and *Ips typographus*) because of their ability to kill large swathes of living trees (Wood 1982). Although these species are commonly intercepted at borders globally, no primary bark beetle has yet established, probably due to the required propagule pressure for establishment, thus I rank primary bark beetles' invasion potential as low-intermediate. Another group of wood infesting beetles are ambrosia beetles, many of which can reproduce parthenogenetically or with siblings, therefore, their Allee threshold is expected to be very low and their invasion potential to be very high. This is reflected in the number of invasive ambrosia beetles intercepted and established worldwide (Wood 1977; Haack 2006; Brockerhoff et al. 2006a; Rabaglia et al. 2008; Hulcr and Dunn 2011). These generalized risk predictions must be taken cautiously, as many species have life history trait associations that span across more than one bark beetle guild.

Intentional management strategies can increase the strength of an Allee effect of invading or newly established invasive populations (Liebhold and Tobin 2008; Essl et al. 2015; Saccaggi et al. 2016). To reduce the number of wood and bark boring propagules transported in wood packaging materials, most countries have implemented phytosanitary measures such as heat treatment or fumigation prior to export (IPPC 2011; Haack et al. 2014). Tactics such as pheromone mating disruption (Sharov et al. 2002; Suckling et al. 2014), aerial insecticide application (Carde and Minks 1995; Brockerhoff et al. 2012), local host destruction (Haack et al. 2010a) and the sterile male technique (Klassen and Curtis 2005; Bouyer and Lefrançois 2014) can be applied to newly established or isolated populations (see Liebhold et al. 2015), assuming an effective strategy is known for a given species. Eradication (the extirpation of an invasive species from a geographical area) of invasive species has a higher probability of success if agencies act immediately upon organism detection (Liebhold and Tobin 2008; Rabaglia et al. 2008; Simpson et al. 2009; Liebhold et al. 2015).

Because Allee effects occur at low population densities, this phenomenon is extremely difficult to observe in nature (Gascoigne et al. 2009). However, by empirically investigating an invasion event, I have been able to demonstrate that positive density dependence can negatively affect the establishment success of founder populations of two bark beetles. Although most transported non-native species fail to establish due to insufficient propagule pressure (Brockerhoff et al. 2014), a few still do. Dispersal via human assistance has drastically increased the number of species moved between continents (Hulme 2009; Liebhold et al. 2012; Eschen et al. 2014) and this trend is not expected to slow down (Levine and D'Antonio 2003; Leung et al. 2014). Therefore, the continuing study of the mechanisms leading to Allee effects that are then applied to management plans are a pressing matter for ecologists, risk decision makers and landscape managers alike.

Chapter 5 – Synthesis and application

The intent of this thesis was to investigate the role of Allee effects during biological invasions of bark beetles, both during the establishment phase and the spread phase that can increase a species range. This work was motivated by the scarcity of empirical evidence demonstrating how Allee effects can prevent small founder population establishment and spread, despite the strong theoretical findings that support this hypothesis (Holt et al. 2004; Kanarek et al. 2013; Walter et al. 2016). In this thesis, I have demonstrated the long range dispersal capabilities (Chapter 2), distribution and range limits in relation to regional pine density in fragmented landscapes (Chapters 2 and 3), and density dependent processes that may affect the invasion success of bark beetles (Chapter 4). I have also provided potential mechanisms of the component Allee effects that are likely to lead to a demographic Allee effect (Chapter 4). I now discuss how the data I have collected in this thesis can more broadly be applied to theoretical ecology, conservation ecology, invasion ecology, and integrated into phytosanitary policies aimed at reducing future forest pest invasions.

The empirical data on species spread and Allee effects in this thesis can be used as baseline data in future theoretical models. The need for empirical data demonstrating Allee effects has long been identified by theoretical ecologists (Courchamp et al. 2000; Keitt et al. 2001; Taylor and Hastings 2005). In Chapter 2, I found direct evidence that both *Hylastes ater* and *Hylurgus ligniperda* disperse at least 25 km and up to 40 km from the nearest large host source (pine plantations). Long distance dispersal was not directly measured for *I. pini* in Chapter 3, but I did find that the most significant predictor of beetle trap capture in relation to spatially weighted averages occurred when large (400 km) regional scales were considered (indicating long distance dispersal is important). My finding that a large pulse of emerging *I. pini* increases local populations in a fragmented landscape above an estimated Allee threshold (Chapter 3) will also be useful for ecologists modeling how rare events are important for determining a species spread and distribution. In Chapter 4, I was able to demonstrate the interaction of two component Allee effects (along with the critical Allee threshold during colonization), leading to a demographic Allee effect in *H. ligniperda* but not *I. pini*, and what traits may explain this difference. I also provided potential mechanisms for the component Allee effects that theoretical ecologists can use with stage-structured models of establishment.

Ecologists concerned with conserving the earth's biodiversity and habitats will also benefit from this study, especially those scientists and decision makers concerned about the effects of habitat fragmentation and the population dynamics of rare and threatened species (Andrén 1994; Hanski 2015). In both Chapters 2 and 3, I found that *H. ligniperda*, *H. ater* and *I. pini* are not dispersal limited in fragmented landscapes, as shown by trap capture in areas with little or no habitat. Instead, these species are restricted by available suitable habitat. However, I also found that *H. ligniperda* and *H. ater* may be

using small patches (pine shelterbelts) in agricultural landscapes as "stepping stones" to move through the landscape (see Appendix B for direct evidence of *H. ater* in roots and root collars of shelterbelt trees). It is possible that successful invaders, such as *H. ater* and *H. ligniperda*, often have traits that allow spread through a fragmented landscape. Further conservation ecological studies should focus on revealing traits of invaders and native species that affect spread through fragmented landscapes. Potentially, the greatest application of my thesis to conservation ecology is the evidence collected showing that probability of establishment is related to initial propagule size. The establishment thresholds I obtained in Chapter 4 can be used to make better predictions about critical release densities for re-introduction and population enhancement.

A major focus of invasion ecologists is determining what traits allow non-native species to become successful invaders. In this thesis, I investigated two successful invaders (*H. ater* and *H. ligniperda*) in one of their invaded ranges (New Zealand) and *I. pini*, a species intercepted but not established outside of its native range (Brockerhoff et al. 2006a), in North America. Traits I found which appear to be associated with *H. ater* and *H. ligniperda* invasion success and spread are long distance dispersal and movement through fragmented landscapes, good host detection post-dispersal, ability to colonize roots and root collars (*H. ater*), ability to colonize firewood and timber (which is then transported by humans), and a relatively small colonization Allee threshold (a small or non-existent Allee effected was detected in tent scenarios for *H. ligniperda* in Chapter 4). Because both *H. ater* and *H. ligniperda* are saprophytes, they may be better able to handle drier phloem conditions during long range transportation of solid wood packaging materials and timber between countries, therefore more likely to arrive in a good physiological state and invade than secondary or primary bark beetles. *Ips pini* appears to have a higher initial colonization threshold but the ability to produce high numbers of F1 beetles at low release densities, offsetting a demographic Allee effect in my experiment (Chapter 4), may make *I. pini* a successful invader one day (Chapter 4). The emergence pulse for *I. pini* described in Chapter 3 is a useful rescue effect mechanism when populations are established, but would not be beneficial during invasion when no reinforcements are available. These observed traits can now be used to improve phytosanitary policies and biosecurity.

The goal of phytosanitary policies is to minimize the number of individual organisms transported, by strengthening current tactics and the innovation of new technologies (Lovett et al. 2016), especially at the pathway level (Leung et al. 2014). Tactics should specifically focus on the probability of transportation of an organism during every step from harvesting of materials, local transportation and storage of materials, conversion of materials to products, long range transportation of products, to arrival in importing countries. This can be done in two main ways: 1) further implementation of, and verifying compliance with, ISPM 15 (heat treatment or fumigation techniques) on solid wood packing materials (SWPM) by countries and companies (Haack et al. 2014). Alternatively, the substitution of SWPM with non-wood based products or wood-based alternatives (e.g. corrugated pallets) was recently estimated to save $36 billion dollars through

2050 (Lovett et al. 2016); 2) restrictions or greater monitoring of the transportation of living plants. It was found that ~70% of harmful forest pests and pathogens established in the USA between 1860 and 2003 probably arrived on living plants (Liebhold et al. 2012). Prevention of future invasive forest pests will depend on the money and efforts afforded to monitor and control these pathways, and should be targeted in areas with increased risk of invasion potential (Liebhold et al. 2013).

I recognize that this thesis is limited by the fact that I investigated only two of many bark beetle species. Further investigations into native saprophytic bark beetles that have been intercepted and never established (e.g. other *Hylastes* spp.) and secondary bark beetles that have invaded novel environments (e.g. *Hylurgops palliatus*, *Ips grandicollis*) need to be conducted to further quantify how Allee effects, and their mechanisms, affect bark beetles with different life histories. Primary bark beetles (a guild I did not study) can undergo population eruptions that result in the mortality of vast swathes of forest (Raffa and Berryman 1983). Therefore, it is of great interest to determine the mechanisms leading to Allee effects in primary bark beetles (e.g., *Ips typographus* and *Dendroctonus* spp.). *Ips typographus* is a frequently intercepted beetle globally, and mortality-inducing *Dendroctonus* spp. are also commonly intercepted, yet, these species have never established (apart from *Dendroctonus valens* which is considered a secondary pest in its native range). Understanding why these and other primary species have been poor invaders in novel environments can further aid our understanding of the life history traits associated with establishment success or failure.

In closing, with the increasing trade and transportation of goods and materials between countries, humans are drastically accelerating the arrival of non-native organisms in novel environments. As a result, the world's ecosystems are facing unprecedented pressures from novel interactions that can result in species loss and the transformation of ecosystem structure and functioning. One exemplary ecosystem that demonstrates the destructive forces of invasive pests are the world's forests, which, in conjunction with the destruction of habitat, are having dramatic consequences on global processes. Globalization of the world's economy is only expected to increase with human population growth and novel organismal and environmental interactions are certain to occur. Fortunately, ecologists are vividly aware of these potential interactions and are working with governments to create policy that reduces the risk of future non-native pest invasions. The work conducted in this thesis indicates that small founder populations will usually go extinct if they remain below an Allee threshold, thus policy aimed at minimizing the number of individuals moved around the world can prevent further incursions and invasions of pests that can potentially cause widespread mortality of our global forests and other ecosystems.

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Appendices

Appendix A - R software code used to create weighted estimates of pine density with a distance decay function in Chapter 2. For this example, random data was generated representing pine density.

```
## Set spatial limits within which the pine density will be calculated

xlim <- 5 # represents 5 cells

ylim <- 5 # represents 5 cells

## Set power parameter (parameter was varied at 0.1, 0.5, 1.0, 1.5, 2.0, 2.5 and 3.0 in this study)

p <- 1.5

## Generate random data

forest <- matrix(rnorm(10000), nrow = 100, ncol = 100) ### random numbers within a 100 x 100 grid (represents a fake forest)

site_x <- c(14, 55, 74) # random coordinates

site_y <- c(27, 84, 49) # random coordinates

## Generate distance matrix - distance measured from focal cell (e.g., an insect trap in regards to this study)

xy <- expand.grid(-xlim:xlim, -ylim:ylim)

dmat <- matrix(NA, nrow = 2 * xlim + 1, ncol = 2 * ylim + 1)

for (x in 1:(2 * xlim + 1)) {

  for (y in 1:(2 * ylim + 1)) {

    dmat[x, y] <- sqrt( ((xlim + 1) - x)^2 + ((ylim + 1) - y)^2 ) # Euclidean distance formula

  }

}

## Form weight matrix
```

```
weight <- 1/(dmat^p)

weight[xlim + 1, ylim + 1] <- 1 # dealing with NA's at focal cell

## Loop through each site (based on 3 randomized sites from above)

estimate <- numeric(length = 3) # 'empty' vector to collect the loop results

for (site in 1:3) {

  # Extract window of data (i.e., the total matrix surrounding each trap)

  windowa <- forest[(site_x[site] - xlim):(site_x[site] + xlim), (site_y[site] - ylim):(site_y[site] + ylim)]

  # Form estimate

  estimate[site] <- sum(weight * windowa)/sum(weight)

  # Inverse distance estimate (sum of 1/d^p Xi divided by sum of 1/d^p)

}

## Output values representing site 1, 2 and 3
estimate
```

Appendix B - Short communication submitted to the New Zealand Entomologist (currently under review) about *Hylastes ater* ability to utilize roots and root collars of windbreak trees in New Zealand.

Evidence of *Hylastes ater* in roots of damaged pine trees in agricultural landscapes and description of a new root herbivore trap

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Running Title: *Hylastes ater* in isolated pine windbreaks

Abstract

Hylurgus ligniperda and *Hylastes ater*, two exotic pine bark beetles in New Zealand, have recently been collected at locations far from pine plantations or other dead pine host material. We wanted to determine if dispersing beetles are reproductively utilizing the roots and root collars of damaged windbreak ('shelterbelt') trees that are common in New Zealand's agricultural landscapes. The ability of these bark beetles to breed in roots and root collars has been noted previously, primarily on dead trees and stumps. But to our knowledge it has not, in New Zealand, been empirically investigated if roots of standing but physiologically declining (i.e. dying) trees can serve as suitable breeding material. We used a novel root herbivore emergence trap to carry out this study, which proved effective. A total of 37 *H. ater* were captured across 13 traps and 3 sites in inland Canterbury; however, no *H. ligniperda* were found. The ability of *H. ater* to colonize roots of damaged and declining isolated pine trees may explain its widespread occurrence in locations far from pine plantations, where windbreaks are acting as 'stepping stones' aiding spread and persistance through the landscape. The apparent absence of *H. ligniperda* in the trees we studied is consistent with its lower abundance in these remote locations, compared with *H. ater*.

Keywords: bark beetle, insect sampling method, invasive species, windbreaks

Introduction

Bark and ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) are one of the most successful groups of invaders in the world (Kirkendall and Faccoli 2010, Aukema et al. 2011). For example, 58 Scolytinae have invaded the United States as of 2010 (Haack and Rabaglia 2013) and more than 6,800 bark and ambrosia beetles were intercepted between 1985 and 2000 (Lee et al. 2007). Invasions by Scolytinae, such as *Ips grandicollis* Eichh. in Australia (Neumann, 1987) and *Dendroctonus valens* LeConte in China (Yan et al. 2005), can have extensive ecological and economic impacts. In New Zealand alone, 11 Scolytinae species have been introduced between 1952 - 2000 (Brockerhoff et al. 2003). Fortunately, no other bark beetles have since become established.

The two most abundant exotic Scolytinae in New Zealand are *Hylurgus ligniperda* Fabricius and *Hylastes ater* Payk., first recorded in 1929 and 1974, respectively (Clark 1932, Bain 1977, Brockerhoff et al. 2006). *Hylastes ater* and *H. ligniperda* are saprophytic species, feeding on dead material of conifers, with a preference for *Pinus* spp. (Scott and King 1973). In New Zealand, both species benefit from abundant breeding material (e.g., stumps and felled logs in contatct with the ground) available in plantation pine forests and the lack of competing wood boring species and specialized natural enemies they would encounter in their native range. Both species can facilitate wood-degrading sapstain fungi (*Ophiostoma* and *Leptographium* spp.) (Reay et al. 2005, McCarthy et al. 2010, McCarthy et al. 2013) and *H. ater* is also known to cause damage in pine plantation seedlings during maturation feeding following emergence (Sopow et al. 2015).

Both *H. ater* and *H. ligniperda* are widespread in New Zealand (Brockerhoff et al. 2006) and have recently been found to occur at long distances (between 25 km and 40 km) from pine plantations (Chase et al., manuscript submitted). One possible mechanism to explain this observation, is the potential for these beetles to utilize not just dead wood but also damaged and stressed windbreak trees in agricultural landscapes. In 1962, Chararas reported the ability of *H. ater* to feed on the root collar and underground roots of standing dead trees (see Fig. 1) (see also Milligan 1978) and *H. ligniperda* is also cited as a root feeding herbivore (Bain 1977, Harrington et al. 2011). However, no studies have directly investigated this behaviour in countries where these beetles are non-native, partly due to the inherent difficulty of investigating root feeding herbivores. Some complex techniques such as acoustic detection and X-ray tomography do exist for detection of root herbivores (see Mankin et al. 2008 for a review of techniques). However, these techniques are quite demanding in terms of equipment and cost, and still require

improvements. For instance, acoustic detection is limited by background sound and range of acoustic signals in soil (Mankin et al. 2008).

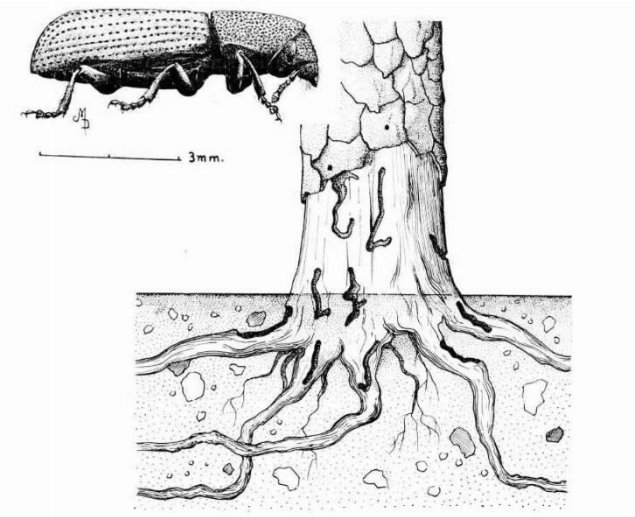

Figure - B1. Depiction of *Hylastes ater* feeding on the roots and root collar of *Picea excelsa* in Europe (Chararas, 1962).

Our objectives in this study were twofold: (1) to confirm if *H. ater and H. ligniperda* breed in underground roots or root collars of damaged windbreak trees in agricultural landscapes and (2) to test the efficiency of a novel trap designed specifically to catch root feeding herbivores. This information advances the understanding of the biological traits associated with the colonization success and spread of species such as *H. ater* and *H. ligniperda* in New Zealand and elsewhere.

Materials and Methods

Study sites

This study was conducted across three different sites in the Southern Alps, New Zealand: Lake Heron station (43 26' S, 171 11' E), Glynn Wye station (42 36' S, 172 28' E) and Grasmere station (43 03' S, 171 45' E). Lake Heron station is located 34 km from the nearest pine plantation. Three traps at Lake Heron were situated in a larger windbreak (~5.5 ha and 730 meters long) and two traps in a ~2 ha and 987 meters long windbreak. Glynn Wye station contains a ~50.0 ha stand of pine forest that has never been harvested. All traps at Glynn Wye were located ~3 km from the pine forest in a ~4.5 ha and 1.3 km long windbreak. Traps installed at Grasmere were within a ~0.5 ha and ~200 m long windbreak. The nearest pine plantation to Grasmere is 11 km away at Craigieburn forest. All windbreak measurements (ha and

length) were obtained from a Google maps area calculator (version 6.11, Daft Logic 2016). The choice of the three studied sites was guided by a previous trapping study (Chase, manuscript submitted).

Trap description

A novel trap was designed specifically for this study (Fig. 2). The trap consisted of a 1.5 m^2 piece of blackout fabric in which two holes were created on each side of the fabric for the installation of two transparent funnels (funnel diameter 80 mm [w] x 100 mm [h] x 9 mm [spout w]), which were secured with a glue gun. On the top of each funnel a lid was glued to allow for the attachment of an insect collection jar (37 mm [w] x 60 mm [h]). A straight line was then cut into the fabric from one corner to the centre such that the trap could be wraped securely around the bole of a tree ~30 to 50 cm above ground level (Figure 2b).

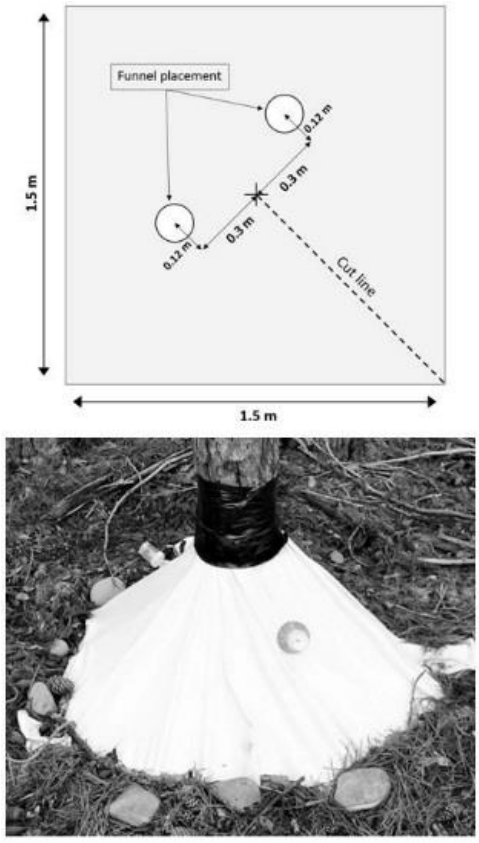

Figure - **B2**. Technical drawing and picture of root herbivore trap used to collect *Hylastes ater* in damaged windbreak trees across agricultural areas of New Zealand.

The top part of the trap was attached to the trunk using iron wire (2 mm) and high tack waterproof duct tape (Pomona R34 duct tape, Auckland, New Zealand). The base of the blackout fabric was strectched

from the trunk to create a conical space underneath, and systematically secured at ground level with large stones and tent pegs. The cut line in the fabric was overlapped on itself and sewn closed to seal the trap completely. This design ensured light only entered through the transparent funnels to attract emerging bark beetles into the collection jars. Prior to installation all collection jars were sprayed with a contact insecticide (Ripcord+, BASF New Zealand, Auckland) in order to kill any insect predators, especially spiders.

Experimental design

A total of 13 traps were installed across the three sites. Four traps were installed at Lake Heron on 5 and 6 November 2015. An additional trap was installed at Lake Heron on a tree with no signs of stress on 24 November 2015 to serve as a control for the study. Four traps were installed at Grasmere on 26 November 2015 and four at Glynn Wye on 1 December 2015. All traps were removed during the week of 8 February 2016.

All traps were placed around trees showing some sign of physiological stress (e.g., top broken, red needles, etc.) or were dying or died recently (except for the control trap mentioned above). We separated stress states into two treatments: 1) stressed but green needles are still present 2) absence of green needles. Pine trees with green needles were assumed to be in a healthier pysiological state than those with no needles or red needles. Tree physiological state was recorded during initial trap installation (Table 1). Traps were checked ~fortnightly, except during the period between 16 December 2015 and 13 January 2016. Upon each check, traps were inspected and any damage fixed; we substituted collection jars with fresh insecticide for old jars and the entry of the funnel was cleaned with a brush to remove any spider webs.

Results

Across all traps, we captured 37 *H. ater* and no *H. ligniperda* (Table 1). Many beetles were caught in the collection jars but we found 17 *H. ater* on the ground near the base of the tree following trap removal. The highest single catch of nine beetles occurred at Glynn Wye between 16 December 2015 and 13 January 2016. *Hylastes ater* was observed in seven of the 13 traps (~54%).

Table - B1 – Trap capture of *Hylastes ater* and tree characteristics at each site

Site and Trap	Installment Date (2015)	Removal Date (2016)	Tree Circumference* (cm)	Tree Damage Characteristics	Green needles 0=Absence 1=Presence	Total number of *Hylastes ater*
Lake Heron 1	5 November	12 February	51	Top broken, no needles.	0	0
Lake Heron 2	5 November	12 February	38	Top broken, green needles.	1	0
Lake Heron 3	6 November	12 February	67	Top broken, dead (no needles).	0	1
Lake Heron 4	6 November	12 February	114	Recently top broken (top part still green).	1	0
Lake Heron 5	24 November	12 February	66	Top broken with green needles.	1	0
Grasmere 1	26 November	10 February	84	Top broken, few red needles remaining.	0	17
Grasmere 2	26 November	10 February	90	Top broken, some green and red needles.	1	1
Grasmere 3	26 November	10 February	86	Top broken, green needles.	1	1
Grasmere 4	26 November	10 February	103	Partly dry red needles (around 40%).	1	0
Glynn Wye 1	1 December	11 February	114	Dry red needles.	0	15
Glynn Wye 2	1 December	11 February	54	Dry red needles.	0	1
Glynn Wye 3	1 December	11 February	114	Green and red needles.	1	0
Glynn Wye 4	1 December	11 February	79	Dry red needles.	0	1

N = 37

* Tree diameter was measured at breast height (i.e. 1.4 m above the ground)

The majority of *H. ater* (86%) captured were in trees in a moderate state of decline, indicated by the presence of red needles. We captured two beetles (5%) from separate trees with green needles but with the tops broken off, indicating that the trees were still alive but in a stressed physiological state. No beetles were found in traps placed around the healthy control tree.

The trap design proved effective for collecting *H. ater* from roots and root collars. Throughout the experiment, the traps stayed in relatively good condition. Only 13% (6 of 47) of the time traps were checked did they need some form of maintenance. The main repairs consisted of reinforcing the base of the trap to the ground. Only one trap at Lake Heron was found totally detached from the ground (14 December 2015). We assume that this damage was caused by strong wind.

Discussion

We confirmed the presence of *H. ater* in the roots and root collars of damaged pine trees within pine windbreaks in agricultural areas far from pine plantations using a novel root herbivore trap design. We did not observe any *H. ligniperda*, although this species has been captured in panel traps placed around pine windbreak areas in Canterbury and is also known to feed and breed in roots and root collars (Fabre and Carle 1975, Bain 1977, Lee et al. 2007).

Hylastes ater is a saprophytic species, therefore, standing trees, even in a moderate state of decline, have not previously been assumed as suitable hosts. However, the majority of trapped *H. ater* in this study came from standing trees that showed symptoms of decline or substantial damage. Surprisingly, we also captured two *H. ater* in trees only recently damaged (top broken, but still exhibiting green needles). The characteristics of these trees that yielded beetles (e.g., decline or considerable damage such as tops broken, and the presence of red needles) can be considered indicators of suitable host material. These findings demonstrate that the range of suitable host conditions for *H. ater* is wider than previously thought.

The detection of *H. ater* from standing trees in isolated areas helps explain this beetle's widespread distribution throughout New Zealand and its presence in remote locations where no typical breeding material (e.g., logging slash) is present. We propose that windbreaks can act like 'stepping stones' that provide *H. ater* breeding opportunities and promote population persistence while moving through the landscape. A similar dispersal mechanism has been investigated with the Asian long horned beetle (*Anoplophora glabripennis* Motschulsky) in South Korea (Williams et al. 2004).

There are pros and cons to all new trap designs, including our prototype. The major advantage of our trap is its capacity to capture any emerging *H. ater* from the roots and root collar of the tree. Even if some beetles have not found their way to the funnel, they can still be collected on the ground during trap removal. To improve beetle catch in funnels, we recommend the use of a course substrate lining (e.g.,

sandpaper). Another useful improvement would be to develop a stronger attachment of the trap to the ground and to remove any vegetation and loose material from the ground before trap installment. It is possible that digging a circular trench and burying the fabric would further ensure beetles could not leave the trap. However, this may be difficult because of the proximity of the trap to the tree with its surrounding roots, especially in windbreak conditions with adjacent trees. Despite the need for minor improvements, the prototype trap has shown to be effective and could therefore be applied to the study of other root herbivores.

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Appendix B References

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